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INVESTIGATIONS OF THE DECLINE OF SWAINSON'S HAWK POPULATIONS IN CALIFORNIA

ROBERT W. RISEBROUGH, RONALD W. SCHLORFF, PETER H. BLOOM
AND EDWARD E. LITRELL

ABSTRACT.—Previous studies have shown that habitat loss is not the principal factor accounting for >90% decline in California populations of the Swainson's Hawk (*Buteo swainsoni*) over the past 80 yr. Swainson's Hawks no longer breed in the southern half of the state, where high levels of DDE contamination may have contributed to, or caused, the extirpation of the species in that area; this hypothesis, however, can no longer be tested. Organochlorine contamination in eggs from central and northern California does not suggest a significant contribution from residues accumulated in South American wintering grounds, nor do present levels of organochlorine contaminants indicate a threat to the surviving California population. Although local population declines continue to occur in California and have also been reported in Oregon and Nevada, other North American populations remain viable. Therefore, mortality during migration, uses of toxic chemicals in South America, or habitat loss on the wintering grounds are not plausible causes of disappearance of the species from southern California. A local factor, or factors, as yet uncharacterized, is indicated.

The Swainson's Hawk (*Buteo swainsoni*), now rare, once occupied a breeding range in California that covered most of the non-forested lowland regions of the state (Bloom 1980). Unfortunately, no quantitative data exist on historical population sizes, but early accounts indicate the species was once very common locally (Sharp 1902). Qualitative information and descriptive generalizations indicate that Swainson's Hawks were so common that most naturalists of the late-nineteenth and early-twentieth century felt the species unworthy of special mention (see Bloom 1980). By the early 1940s, the population was declining (Grinnell and Miller 1944) and by 1978 the species was a scarce breeding bird in California. Bloom (1980) found that the population had fallen from a conservative estimate of 4300 pairs at the beginning of the century to <400 pairs in 1979, a loss exceeding 90%. Breeding distribution also had been greatly reduced and the species has disappeared from the southern part of the state (Fig. 1). The last recorded nestings were in the Mojave Desert in San Bernardino and Los Angeles counties in 1979 and 1980, respectively (P. Bloom, unpubl.). Between 1980 and 1988, 3-8 breeding territories have been active in Inyo and Mono counties (P. Bloom, unpubl.; Fig.

1). In this paper we address the hypothesis that exposure to persistent organic contaminants, either in California or in South America, has adversely affected the population of Swainson's Hawks in California, and we review other possible causes of the population decline.

STUDY AREA AND METHODS

In July 1979 we collected 1 addled egg from each of 3 nests that contained 1-3 young, and 3 eggs with dead embryos from 1 nest in the Great Basin in northern California (Siskiyou and Modoc counties). Habitat in this area is characterized by juniper (*Juniperus occidentalis*) and big sagebrush (*Artemesia tridentata*). An additional addled egg was obtained in 1979 in the Mojave Desert, San Bernardino County, in Joshua tree (*Yucca brevifolia*) habitat, one of the 2 last known nestings of the species in California south of the San Joaquin Valley (P. Bloom, unpubl.). In April and May of 1982 and 1983, 1 fresh egg was taken from each of 8 Swainson's Hawk nests in the Central Valley (Yolo, Sacramento, Sutter, and San Joaquin counties). Collection sites were in agricultural areas interspersed with riparian and oak woodland habitat containing cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*) and willow (*Salix* sp.). Fresh eggs were collected from each nest as rapidly as possible to ensure that the remainder of the clutch would not suffer lethal chilling or heating. The resulting 15 egg sample was therefore representative of greatest Swainson's Hawk nesting density in California

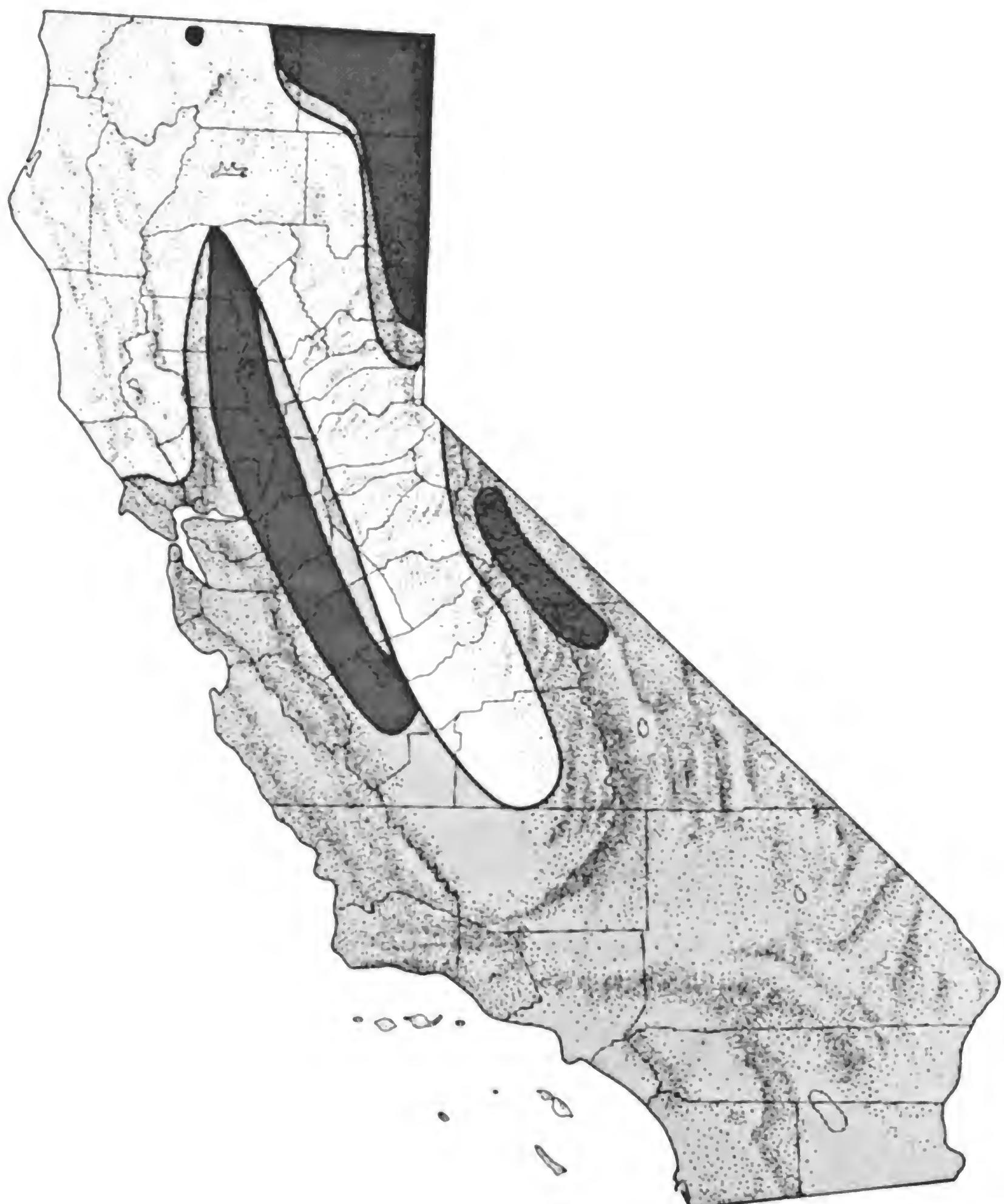


Figure 1. Breeding range of the Swainson's Hawk in California during the late nineteenth and early twentieth centuries (stippled area) and in the 1980s (shaded area). From Schlorff and Bloom (1983).

Since no statistical tests were performed with an assumption that residue composition is affected by the state of the egg, whether addled or fresh, all data are considered together; moreover, Ambrose et al. (1988) recorded no difference in residue composition between addled and fresh eggs within Peregrine Falcon (*Falco peregrinus*) clutches.

Analytical Methods. Eggs obtained in 1979 were analyzed at the University of California. Egg contents were mixed with anhydrous sodium sulfate and soxhlet-extracted with methylene chloride. After removal of methylene chloride by rotary evaporation, lipids were dissolved in hexane. For clean-up, up to 0.5 g lipid was placed on a florisil column that had been pre-rinsed with hexane (florisil activated overnight at 165°, cooled, deactivated with 0.5% H₂O, 33 g florisil, column ID 20 mm). Three fractions were collected, eluting with hexane (F1), 30% methylene chloride in hexane (F2), and 50% methylene chloride in hexane (F3). Volumes were adjusted such that DDE but not DDT eluted in F1, DDT but not dieldrin eluted in the F2, and dieldrin eluted in the F3.

Extracts were analyzed with Carlo Erba 2350 and 4160 gas chromatographs equipped with Carlo Erba and Brechbuhler electron capture detectors. Two columns, 30 m fused silica DB1 and DB5 (J&W Scientific), were used in the course of the study. Injections were on-column. After an initial hold for 3 min at 45°, runs were programmed at 10°/min to 140°, and at 4°/min to 290°. Carrier gas was helium. Compounds reported were quantified initially on the basis of electron capture response of decachlorobiphenyl (DCB), which was added as an internal standard, then by applying a factor based upon electron capture response of authentic standards supplied by the U.S. Environmental Protection Agency. Extract volumes were reduced to 100 microliters or less to increase analytical sensitivity which ranged from 0.1–0.5 ng/g (ppb) of individual compounds except when interfering compounds co-eluted on both column types employed.

Samples obtained in 1982–1983 were analyzed at the California Department of Fish and Game Fish and Wildlife Water Pollution Control Laboratory, Rancho Cordova. Five-g subsamples of egg contents were ground with anhydrous sodium sulfate and blended with two 150 ml portions of petroleum ether. After vacuum filtration, volumes were adjusted to 250 ml. A 200 ml aliquot was evaporated to dryness to determine lipid content. The remaining 50 ml aliquot was passed through a florisil column and eluted with 200 ml petroleum ether, 200 ml 6% ethyl ether in petroleum ether, and 200 ml 15% ethyl ether in petroleum ether. Eluates were concentrated to 10 ml, and analyzed with a Varian Aerograph 370 gas chromatograph equipped with a Ni⁶³-electron capture detector. Lower limit of detection was 10 ppb for individual compounds.

A calculation of approximate fresh weight (Stickel et al. 1973) was made for the 1982 and 1983 samples. No reduction in weight due to moisture loss was noted and no conversion was made.

An intercalibration carried out between the 2 laboratories over approximately the same time period revealed satisfactory agreement in measurements of DDE and PCB in a series of Peregrine Falcon eggs (Peakall et al. 1983). Shell thicknesses were measured at the Western Foundation of Vertebrate Zoology, Los Angeles, to the nearest

0.001 mm with a Federal bench comparator thickness gauge.

RESULTS AND DISCUSSION

Population Decline and Productivity. Swainson's Hawk populations in Wyoming and Alberta do not appear to have undergone a decline comparable to that which has occurred in California (Dunkle 1977; Fyfe 1977; Schmutz 1984). Similar declines, however, have been reported from Nevada (Oakleaf 1975; Oakleaf and Klenbenow 1975; Oakleaf and Lucas 1976; Herron and Lucas 1978) and in southeast Oregon (Littlefield et al. 1984). In the latter area Swainson's Hawks had formerly been the most common nesting buteo in the Malheur-Harney Lakes Basin, but became uncommon after the 1950s. In the 1960s the number of breeding pairs ranged between zero and 5 in the Malheur National Wildlife Refuge, and in the 1970s there were no nesting pairs in most years (Littlefield et al. 1984).

No reduction in productivity has been recorded in Oregon (Henny et al. 1984; Janes 1987), but in the Klamath Basin in northern California fewer than 50% of the active territories produce young and fewer than 50% of territories previously known to be active were active in the mid 1980s (P. Bloom and S. J. Hawks, unpubl.).

Shell Thinning. Using an estimate of 0.402 (S.D. = .032) mm for the pre-1947 thickness of Swainson's Hawk eggshells from California, a mean reduction of 4% in shell thickness among the sample of 14 eggs (Table 1) was not significant ($P > 0.05$; Student's *t*-Test). Henny and Kaiser (1979) estimated a pre-1947 thickness from measurements of 31 eggs from Oregon, Washington, and Idaho of 0.428 (S.D. = 0.028) mm, 6.5% higher than our estimate for eggs from California. Three eggs collected in 1976 near a DDT spray area in northeast Oregon showed a mean reduction in shell thickness of 11% and contained 4–7 ppm DDE (Henny and Kaiser 1979). In a study undertaken in the Columbia Basin in Oregon in 1978–1980 to assess the extent of heptachlor epoxide contamination, 25 eggs, each obtained from separate nests, averaged 9.6% reduction in shell thickness from the estimated pre-1947 mean of 0.428 (Henny et al. 1984).

Since both estimates of pre-1947 thicknesses were derived from measurements made at the Western Foundation of Vertebrate Zoology using a bench comparator thickness gauge, the difference between pre-1947 estimates does not derive from differences

Table 1. Shell thickness of Swainson's Hawk eggs from California.

LOCALITY	YEAR	N	MEAN THICKNESS (S.D.)
California	pre-1945	40*	0.402 (0.032)
Klamath Basin	1979	5	0.399 (0.028)
San Bernardino Co.	1979	1	0.378
Central Valley	1982	3	0.400 (0.033)
Central Valley	1983	5	0.363 (0.013)
California	1979-83	14	0.385 (0.028)

* Data provided by Western Foundation of Vertebrate Zoology.

in measuring techniques and most likely derives from geographical differences in pre-1947 thickness over California, Oregon, Washington and Idaho. Using the pre-1947 estimate of Henny and Kaiser (1979) would increase the mean level of thinning in the California sample to about 10%, comparable to that reported by Henny et al. (1984) in eggs from the Columbia Basin.

A review of eggshell thinning and population status has shown that thinning above 18% is invariably associated with population decline (Anderson and Hickey 1972; Lincer 1975). Productivity of Prairie Falcons (*Falco mexicanus*) in Alberta, however, declined to zero over a range of 8-14% reduction in Ratcliffe thickness index (see Ratcliffe 1967; Fyfe et al. 1988); reduced productivity of Golden Eagles

(*Aquila chrysaetos*) in western Scotland was associated with a 10% reduction in thickness index (Lockie and Ratcliffe 1964; Lockie et al. 1969; Ratcliffe 1970). A 10% reduction of mean thickness does not therefore indicate normal productivity. As noted above, no reduction in productivity has been recorded in Oregon.

Organochlorine Residues. Geometric mean DDE levels in eggs from the Great Basin and the Central Valley were <1 part per million (ppm) (Table 2), lower than geometric means of 1.2 ppm in 6 eggs from southeast Washington in 1976 and 2.3 ppm in 4 eggs from northeast Oregon in the same year (Henny and Kaiser 1979). Three of the latter eggs ($\bar{x} = 5.4$ ppm) were from an area adjacent to forests treated with DDT 2 yrs previously, and elevated residues were attributed to that source. The 25 eggs obtained in Oregon in 1978-1980 contained a (geometric) mean level of 0.98 ppm DDE (Henny et al. 1984). A sample of 5 addled eggs obtained in southeastern Washington in 1977 and 1978 contained a mean DDE level of 0.92 ppm (Bechard 1981). Four eggs from 3 nests at the Hanford Site in Washington in 1976 contained substantially higher levels (range = 4-17 ppm; Fitzner 1980). Sixteen eggs (1/clutch) from North and South Dakota over 1974-1979 all contained <1 ppm DDE (Stendell et al. 1988). Except for higher values at the Hanford site and the site adjacent to DDT spraying operations in Oregon, DDE levels were therefore com-

Table 2. Organochlorines (ppb of wet weight) in eggs of Swainson's Hawks from California. Values are geometric means of clutch arithmetic means, with an interval of 1 standard deviation.

LOCALITY	N	% H ₂ O	% LIPID	<i>p,p'</i> - DDE	<i>p,p'</i> - DDD	<i>p,p'</i> - DDT	DIEL- DRIN	HCB	PCB	HEPT. EPOX
Klamath Basin	4	78	6.0	780	18	27	100	11	45	51
		75-81	4.7-7.7	320-1900	7-48	2-100	55-180	5-25	30-68	31-82
San Bernardino County	1	76	4.7	7900	34	24	75	13	67	16
Central Valley	8	nm*	3.8	910	<10	<10	57	3	<100	17
			3.0-4.8	460-1800			32-100	1-11		4-76
LOCALITY		<i>t</i> -NONA- CHLOR	OXYCHLOR- DANE	γ -CHLOR- DANE	α -CHLOR- DANE	ENDRIN	α -HCH	β -HCH	γ -HCH	
Klamath Basin		27	37	3	4	33	<2	12	<1	
		9-77	7-200	1-7	1-10	22-59		3-50		
San Bernardino		11	12	0.9	<4	20	0.7	12	0.6	
Central Valley		12	18	nm	nm	nm	nm	nm	nm	
		7-19	7-36							

* nm = not measured.

parable over Washington, Oregon, and northern and central California over 1976–1983.

A single egg from southern California from one of the 2 last known nestings in the area contained 7.9 ppm DDE and had a thickness reduction of 6% (Tables 1 and 2). The DDE level is within range of DDE concentrations associated with reproductive failures of Prairie Falcons (Fyfe et al. 1988), Bald Eagles (*Haliaeetus leucocephalus*; Wiemeyer et al. 1984), and higher than the 5 ppm level associated with 20% thinning of California Condor (*Gymnogyps californianus*) eggs (Kiff et al. 1979). Henny et al. (1984) found, however, that productivity was high in 5 Swainson's Hawk nests from which single eggs taken for analysis contained between 5 and 10 ppm DDE. The threshold of sensitivity to DDE (see Fyfe et al. 1988) appears therefore to be higher for Swainson's Hawks than for these species.

The contaminant profile in the single egg mentioned above was similar to that recorded in several other recent studies of organochlorine contamination in the Southwest that have been characterized by high levels of DDE and high ratios of DDE to all other compounds, including the parent compound, p,p'-DDT (Cain and Bunck 1983; Clark and Krynnitsky 1983; White and Krynnitsky 1986; Hunt et al. 1986). DDE levels in both terrestrial and marine environments of southern California have remained high throughout the 1980s (Hunt et al. 1986; Risebrough 1987; Kiff 1989; Garcelon et al. 1989; R. W. Risebrough and P. H. Bloom, unpubl.), a legacy of past disposal of wastes from a DDT factory in Los Angeles (Risebrough 1987; Young et al. 1976).

A South American "Signature"? Comparison of contamination patterns, characterized as the ratio of DDE to other organochlorines, with those in eggs of Peregrine Falcons from California and Alaska over the same period (Table 3) suggest but do not conclusively indicate a South American component in the profile. Peregrines breeding in Alaska, which migrate to South America and take among their prey many species which also migrate to South America, contained significantly higher ratios of dieldrin, DDT+DDD, endrin, heptachlor epoxide, trans-nonachlor, mirex, and beta-HCH to DDE than the resident birds of California (Springer et al. 1984). Relatively high amounts of dieldrin were recorded in Swainson's Hawk eggs examined, at levels 8–16 times below those of DDE (Table 3). Dieldrin is no longer used in California; nor is aldrin, which converts to dieldrin in the environment. Aldrin is used

Table 3. Ratios of DDE to other organochlorines in eggs of Peregrine Falcons from California, 1975–1980,* Alaska, 1977–1980* and in eggs of Swainson's Hawks analyzed in this study.

COM- POUND(S)	PEREGRINE FALCON		SWAINSON'S HAWK	
	ALASKA	CALI- FORNIA	KLA- MATH BASIN	CENTRAL VALLEY
N	8	12	4	8
DDD + DDT	150	350	17	>45
Dieldrin	19	180	8	16
HCB	570	380	71	300
PCB	3.9	3.2	17	>9
Hept. Epox.	36	300	15	54
t-nonachlor	510	1900	29	76
Oxychlordane	72	87	21	51
Endrin	780	1900	24	—
beta-HCH	93	520	65	—
mirex	90	1000	800	—

* Data from Springer et al. (1984).

in South America to control species of leaf-cutting ants which are destructive to many crops (Risebrough and Springer 1983; Burton and Philogene 1986), and the presence of relatively high levels of dieldrin could indicate a South American source. Relative amounts of DDT+DDD, PCBs, heptachlor epoxide, endrin, and beta-HCH are also typical of a South American profile. Relative levels of mirex, however, are low. Mirex is also extensively used in South America to control leaf-cutting ants. Levels of mirex in species such as American Kestrels (*Falco sparverius*) in southern Brazil may be equivalent to those of DDE (A. M. Springer and R. W. Risebrough, unpubl.). Concentrations of mirex were higher in eggs of Peregrine Falcons that had migrated to South America than in eggs of peregrines resident in California where mirex is not used (Springer et al. 1984). Western Sandpipers (*Calidris mauri*) collected at 2 sites in California in 1980 during spring migration contained mirex at levels in the order of 15% of DDE (Risebrough, unpubl.).

Mirex is therefore a potential "marker" compound for South America origins of organochlorine mixtures. Like the DDE:PCB ratio, which tends to be conservative within an ecosystem when the PCB consists primarily of the penta-, hexa-, and heptachloro compounds (Risebrough et al. 1968; Norstrom et al. 1978), the DDE:mirex ratio is

also relatively conservative in ecosystems (Norstrom et al. 1978). Mirex was detected at low concentrations (in the order of 1 ppb) in 2 eggs from the Klamath Basin. The DDE:mirex ratio would be in the order of 800, closer to the ratio of 1000 found in the eggs of California Peregrine Falcons than ratios of 28-110 found in eggs of Peregrine Falcons in Alaska and Greenland (Springer et al. 1984).

We find therefore suggestions but no convincing evidence for a South American "signature" of organochlorine residues in California Swainson's Hawk eggs. Such a signature may, however, be partially obscured by the contaminant profile of local prey. Nor is there evidence for excessive exposure to aldrin/dieldrin or heptachlor/heptachlor epoxide that might suggest mortalities on wintering grounds caused by these biocides. Argentina, where many Swainson's Hawks winter (Brown and Amadon 1968; Houston 1968; White et al. 1989), has adopted controls on the use of most organochlorine insecticides similar to those of North America; comparable restrictions have been adopted in the neighboring Brazilian state of Rio Grande do Sul (Risebrough and Springer 1983).

Other Potential Causes in South America of Population Decline. Shooting during migration can be devastating to roosting flocks (Bloom 1980). Loss of wintering habitat is poorly studied; in southeastern Brazil large areas of grassland have recently been converted to soya bean cultivation (Albuquerque 1978), a change likely to have affected available habitat. Several of the newer-generation organophosphates and carbamates that are highly toxic to birds include famphur (Franson et al. 1985; Henny et al. 1985; Henny et al. 1987), carbofuran (Balcomb 1983) and fenthion (Henny et al. 1987). Documentation is lacking, however, on possible effects in Latin America.

There is no evidence for regional partitioning of wintering range that might account for local population declines in North America. Among 23 band returns from Argentina, 3 were from Colorado, 1 from Wyoming, 7 from Alberta, and 8 from Saskatchewan (White et al. 1989).

Interspecific Interactions. Among possible causes for the decline in southeast Oregon proposed by Littlefield et al. (1984) was a local abundance of Great Horned Owls (*Bubo virginianus*). Fitzner (1978) has reported a low tolerance of Swainson's Hawks for Great Horned Owls. In Oregon, Janes (1987) has documented intense interspecific terri-

torial encounters between Swainson's Hawks and Red-tailed Hawks (*Buteo jamaicensis*). In these Swainson's Hawks were frequently dominant in spite of their smaller size and would displace Red-tails from territories with a low density of perches and outcrops. Red-tails successfully defended, however, territories with a higher density of perches and outcrops. Human settlement has increased the numbers of available perches in trees and on utility poles, thereby favoring Red-tails over Swainson's Hawks (long-term) in habitat suitable for both species (Janes 1987).

We consider it unlikely that interspecific competition would result in the disappearance of the Swainson's over all of southern California. Nor does predation by a high density of Great Horned Owls in southern California appear plausible. Of more than 1000 nests of Red-tailed and Red-shouldered Hawks (*B. lineatus*) examined in the region, only 1 failure could be attributed to Great Horned Owl predation (P. Bloom, unpubl.).

Habitat Loss and Modification. In southeast Oregon native grasses have disappeared because of overgrazing; sagebrush has become the dominant plant, forming large monotypic stands in some areas and reducing the number of foraging sites (Littlefield et al. 1984). Prey vulnerability is reduced; Bechard (1982) has reported that hunting sites of Swainson's Hawks in Washington were determined more on vulnerability of prey to predation than on prey density.

Breeding habitat in the Central Valley of California and elsewhere has been lost due to agricultural conversions. Some 1,400,000 acres of riparian habitat in the Central Valley have been destroyed since pre-settlement times, an 85% loss (Smith 1977). Elsewhere, however, breeding populations have disappeared in the absence of environmental changes, and large areas of formerly occupied breeding habitat in the Central Coast Ranges, the Mojave Desert, the Great Basin, Owens Valley and the Southern California coastal area still exist (Bloom 1980, Schlorff and Bloom 1983). Thus, although a contributing factor, particularly in the Central Valley, habitat destruction on breeding grounds is probably not the principal reason for extirpation of the species in the southern half of the state.

Impact of Organochlorines on Other *Buteo* Species. Generally, raptorial species that feed like the Swainson's Hawk on small mammals, reptiles and invertebrates (Bloom 1980; White et al. 1989)

have shown only a relatively small degree of shell thinning (Anderson and Hickey 1972); non-bird-eating species generally accumulate lower residues of organochlorines than bird-eating species (Gilbertson and Reynolds 1974). Common Buzzards, (*B. buteo*), however, suffered severe population declines in the Netherlands in the 1960s that were attributed to dieldrin (Fuchs et al. 1972).

Low-to-moderate shell thinning has been reported in apparently only 2 other species of the genus *Buteo*, the Red-shouldered Hawk (Anderson and Hickey 1972; Wiley 1975) and the Red-tailed Hawk (Anderson and Hickey 1972). Analysis of banding records of Red-shouldered Hawks has indicated lower recruitment during the years of heavy DDT use in North America (Henny 1972). Counts during migration indicated population declines in eastern North America at that time (Hackman and Henny 1971; Brown 1971). This is apparently the only documented decline of a species of *Buteo* during the DDT era in North America that can plausibly be attributed to DDE.

Summary. In California, only the Least Bell's Vireo (*Vireo bellii pusillus*) (Remsen 1978) and the California Condor (Wilbur 1980; Kiff 1989) have experienced more severe population reductions. After a severe reduction in the 1960s (Herman et al. 1970), Peregrine Falcons are now rapidly recovering (Walton et al. 1988). The hypothesis that high levels of environmental DDE were the major cause of disappearance of the Swainson's Hawk in southern California remains plausible. In the current absence of any breeding Swainson's Hawks in the area, it is no longer subject to testing. It is likely, however, that the cause of the extirpation in southern California is related to the decline in Nevada and southeast Oregon, and most likely to the report of depressed productivity in the Klamath Basin area of Northern California (P. Bloom and S. J. Hawks, unpubl.).

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CENSUSING OF DIURNAL RAPTORS IN A PRIMARY RAIN FOREST: COMPARATIVE METHODS AND SPECIES DETECTABILITY

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ABSTRACT.—No reliable method has ever been proposed to census a rain forest raptor community. I investigated 4 methods in primary forest of French Guiana and compared results; 1) Mapping territorial pairs, displaying over canopy and followed from dominant lookouts, gives the most complete data on regularly soaring species (*Harpagus*, *Buteogallus*, *Spizaetus*, *Spizastur*); 2) mean instantaneous number of birds flying over a definite area in optimum conditions may be a reasonable density estimate for vultures (Cathartidae); 3) mapping of individuals recorded along a regular network of trails in the understory was only successful for the highly conspicuous Red-throated Caracara (*Daptrius americanus*); 4) density estimates from understory strip transects were consistent with those obtained by other methods for 6 of 8 species. Specific detectability, soaring behaviors and frequencies of display flights varied widely among species and so did time required to assess the existence of a territorial pair (1–7 d). Marking, radiotracking and playback of vocalizations are promising techniques but are very time consuming and more appropriate for a detailed study of particular pairs than for survey of a whole community. Use of an abundance index, with a distinct technique for each species, may avoid biases of density estimates.

Birds of prey are notoriously difficult to survey in tropical forests, especially in tall, dense, large unbroken tracts of humid lowland forest. No complete census of a rain forest raptor community, with density estimates over a significant area, has ever been published and no appropriate methodology has even been proposed. However, many rain forest raptors are now threatened by habitat destruction, disturbance or fragmentation (Thiollay 1985b). Raptors may be suitable indicators of optimum size of a forest reserve, because raptors are likely to require areas larger than most other species. Yet, there is still an urgent need of basic data on natural distribution and density of rain forest raptors because of a concern about the suitability of many reserves or even national parks which may well prove to be too small for long term survival of some raptor species supported originally.

As part of a larger study on design of a national park in French Guiana, I assessed the distribution and relative abundance of raptors over the country's 80 000 km² rain forest area, and I estimated the density of every species within a representative 100 km² sample quadrat (Thiollay 1989).

Life history and behaviour of most rain forest raptor species are very poorly known, if at all (Thiollay 1985a). Often only scant information comes from marginal habitats, rather open woodlands or edges where a species' biology may be atypical. After 20 yrs of personal experience in both New and Old World tropical forests, I can testify that nests of

many species are almost impossible to find in primary forest, except under extraordinarily lucky circumstances. In fact, for many species, the nest has never been described. Several species, including some of the most common neotropical forest raptors, seem to never soar(?) nor even fly over the canopy and very rarely venture outside the understory. Although not particularly shy, most species are very secretive and spend long periods perched motionless. Many are very vocal, but others are usually silent. Density is often low and distribution very patchy, which further decreases rate of encounters.

Thus, most raptor-specific census methods (see review in Fuller and Mosher 1981), devised for temperate species, cannot be applied directly to tropical forest species. Nevertheless, I have tried to adapt classical concepts to propose empirical methods that need further improvement and testing in similar situations. My attempts are preliminary, and as such, voluntarily unsophisticated. No single method can be appropriate for every species, and 2 or more different techniques should always be used concurrently.

In this paper I concentrate only on comparative results of complementary methodologies. Biological and conservation significance of the data are developed elsewhere (Thiollay 1989).

STUDY AREA AND METHODS

After 5 yrs of raptor surveys throughout French Guiana, I tried to obtain a quantitative estimate of

the density of every raptor species within as large a representative area as possible.

Around the Nouragues field station, in north-central French Guiana ($4^{\circ}05'N$, $52^{\circ}41'W$), a 100 km^2 quadrat of primary forest was chosen within a much larger expanse of similar unbroken lowland rain forest. The area was hilly, crossed by small rocky watercourses, and ranged in altitude from 27–413 m. Also included were sizeable tracts of every forest type encountered in Guiana, except cloud forest. The quadrat was centered around 2 large natural openings, with small field stations nearby: a medium-sized river in the south and a large granitic inselberg in the northern part provided the most convenient observation sites (Fig. 1).

The survey took place in the driest season, from early September to mid-October 1986 and 1987 over a total of 73 d of intensive field work with unusually fine weather conditions. From the little information available (Haverschmidt 1968 and pers. obs.), most raptors were either breeding or ending their reproductive cycle (feeding fledged young). All were assumed to be sedentary with an extended period of breeding activity and a permanent pair bond and territory occupancy.

Different census methods have been adapted to the behavior of individual species. Methods are here proposed as preliminary suggestions. Comparative results will be used as a test of reliability. As the coverage was better, more intensive and frequent around field stations and large openings, 2 better known areas were distinguished (Fig. 1). *Zone I* (6 km^2) included the inselberg and its lookouts, the main field station and its clearing as well as a dense network of trails. Every species present was assumed to be recorded and reasonably well mapped (no new data during the last 30 d.). *Zone II* (42 km^2 including *Zone I*) was centered around the inselberg and covered a 3-km rad area around the 4 outmost lookouts of the mountain top from which only soaring species were mapped. A 3-km rad was the maximum distance at which large raptors were accurately identified and located with 10×40 binoculars and $11-33 \times$ telescope.

The entire study area (100 km^2) was visible from the top of the inselberg but only the largest raptors could be seen beyond *Zone II*. However, most outer regions were in sight above canopy within 2.5 km of 9 additional lookouts (riverbanks and large treefall gaps on ridges or steep slopes). The quadrat was divided into $1 \times 1\text{ km}$ squares, of which 70 were

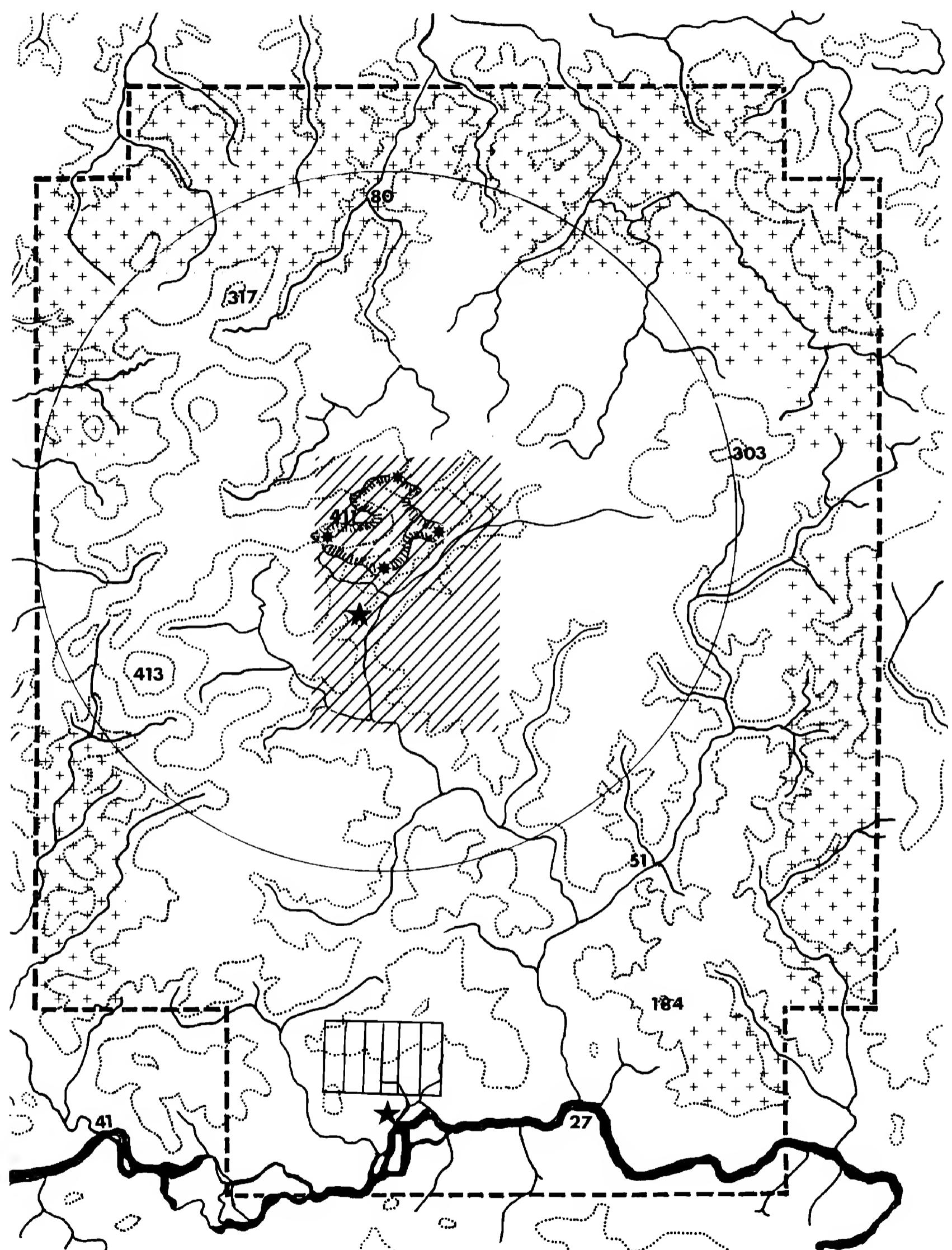
crossed by foot at least twice, including 35 outside *Zone II*.

Mapping of Soaring Birds. One group of species regularly soar above canopy and may then be easily detected from outside the forest or through large openings: Gray-headed Kite (*Leptodon cayanensis*), Hook-billed Kite (*Chondrohierax uncinatus*), Rufous-thighed and Double-toothed Kites (*Harpagus diodon* and *H. bidentatus*), Tiny, Bicolored and Gray-bellied Hawks (*Accipiter superciliosus*, *A. bicolor* and *A. poliogaster*), White Hawk (*Leucopternis albicollis*), Great Black Hawk (*Buteogallus urubitinga*), Crested Eagle (*Morphnus guianensis*), Black and White Eagle (*Spizastur melanoleucus*), Black and Ornate Hawk Eagles (*Spizaetus tyrannus* and *S. ornatus*). Soaring behavior performed by adults on their breeding grounds has mainly a territorial function (surveillance and maintenance of pair bond or territorial limits, Newton 1979). Soaring is often accompanied by loud calling, nuptial display or intraspecific aggression. I assumed that adults, especially when displaying, flew mostly, if not only, over their own territory.

A large, bare, rocky outcrop protruding 200 m over the surrounding forest offered an ideal vantage point. Four convenient lookouts were chosen on the outermost parts of the inselberg, each offering an unrestricted 180° view. A total of 167 hr was spent overlooking the forest in fine weather and mainly during the optimal morning hours (0900 H–1200 H). The marked relief facilitated the location of flying birds.

All raptors seen flying over the forest (or perched on emergent dead trees) were followed and their itinerary carefully mapped (1/50 000 scale). Day after day, the data were superimposed, soon giving a picture of clearly separated ranges for most species. So-called territories were derived by the minimum convex polygon method (Ford and Myers 1981; Southwood 1966) connecting the outermost points reached by birds under observation. Territory size was determined using a planimeter and correcting for small sample size biases by the method of Jenrich and Turner (1969). Adjacent territories were discriminated by simultaneous observation of the 2 pairs involved.

Over 20 complete flight circuits were drawn for at least 1 pair of the 5 most common and conspicuous species (*H. bidentatus*, *L. albicollis*, *B. urubitinga*, *S. melanoleucus* and *S. ornatus*). Each pair yielded rarely more than 1 circuit/d. No new information was



obtained after the 5–10 circuits plotted initially. Thus, sample size was probably large enough to avoid an underestimation of territory size (Ford and Myers 1981).

Population Estimates of Species Hunting Over the Forest. Another group of raptors fly above canopy to search for carrion (vultures) or hunt for insects (kites) and birds (falcons). Each group is easily detected but wide ranging and may be occasionally gregarious.

The most common species in the group is the Greater Yellow-headed Vulture (*Cathartes melambrotus*) which wanders throughout the area and temporarily concentrates around carcasses. Particular pairs could not be separated. For want of a more accurate estimate, I have recorded during 20 hr in the late morning (0900 h–1200 H) period, the mean number of individuals crossing a 10 km² area/hr. The 20-hour data, extrapolated to the larger study area, are in good agreement with the largest concentration of birds seen during the course of the study.

A similar estimate has been computed for the King Vulture (*Sarcoramphus papa*) and the Swallow-tailed Kite (*Elanoides forficatus*), both of which wander great distances; the former solitarily or in pairs and the latter in flocks. Additionally, resident families were recognizable and their roost sites located.

The Plumbeous Kite (*Ictinia plumbea*) is well distributed over the area in isolated pairs which occasionally join nomadic groups of *Elanoides* but are otherwise rather territorial. Plumbeous Kites have been mapped according to the previous method and a small floating population, inferred from rare concentrations observed, has not been considered. One pair of Orange-breasted Falcon (*Falco deiroleucus*) was attached to the only suitable cliff.

Specific Daily Soaring Activity. Each species had its own pattern of soaring behavior and hence a different detection probability. To assess daily flight pattern and time during which each species was visible, I define a fixed 10 km² area (i.e., a 2.5 km

rad on a 180° field, the largest area manageable for this purpose), from the western lookout of the inselberg. I divided daylight hours (between sunrise and sunset) into 4 periods. Each period was covered during 17–20 hr. (fine weather only). Within each hour observation, the following parameters were recorded: 1) minimum number of different individuals seen; 2) total time (min) where at least 1 bird was flying over the area; and 3) behavior of each individual (soaring, hunting, displaying, . . .). Besides vultures, whose home ranges were difficult to define, all 12 soaring species were represented by 1 resident pair on the 10 km² area (either >50% of their territory included in the area or a larger territory covering >50% of the area).

The number of flying raptors slowly increases from sunrise to 0900 H, then quickly reaches a maximum between 1000 and 1100 H, and decreases almost continuously after noon. However, vultures remained very active up to about 1600 H and kites were even most active in mid and late-afternoon when no rain had occurred.

Understory Censuses. The Forest Falcons (*Micrastur*), the Black-faced Hawk (*Leucopternis melanops*) and, to a lesser extent, the Red-throated Caracara, rarely fly high over the canopy. Caracaras are very noisy but Forest Falcons usually call mostly at dawn and *Leucopternis* is not often heard. The Harpy Eagle (*Harpia harpyja*) is only conspicuous when sun-bathing on emergent dead trees in early morning. Since it was necessary to scour the forest to find these species, I tried to use sightings in 2 different ways. For soaring species understory records were compared to results of the above mapping method.

I first walked along a network of trails in the understory, 100 km long, designed to pass within 500 m of every point. Thirty km were already laid out through the undergrowth, mostly in Zone I. Remaining "trails" were only outlined by a white thread at breast height. I moved slowly, focusing my attention exclusively on raptors and recording every



Figure 1. Topography of the 100 km² study area: main watercourses (unbroken lines), 100 m contour lines (dotted lines), maximum and minimum altitudes (meters asl), little wooded part of the rocky inselberg (hatched contour). The circle features the 42 km² area covered by a 3 km-rad around the 4 outmost observation points around the inselberg's summit (asterisks). The hatched rectangle is the 6 km² most intensively surveyed area. Stars indicate the field stations and the rectangular network is the intensive study trails near the southern station. Peripheral stippled squares have been crossed by foot only once, if ever.

observation on a map at the nearest 100 m. The area to be covered was too large and the density of birds was too low to obtain enough records and an accurate mapping of territorial pairs outside the most intensively searched area.

The second method was to use the data for a tentative density estimate of all individuals. The most rigorous technique should have been a line transect sampling [i.e., recording along a straight line sighting and perpendicular distances, as well as sighting angles, of every bird seen]. A density estimate may then be derived through a probability function at zero distance from the line. This is obtained by fitting, to the perpendicular distance data collected, Fourier series models which best meet the estimator shape and goodness of fit criteria (Burnham et al. 1980; Brennan and Block 1986). Unfortunately, the first assumption of line transect theory, that all birds on the line must be seen with probability 1, is not always met since raptors initially perched just along the transect can escape undetected well ahead of the observer. Most of all, no reliable density can be statistically estimated without at least 40–60 observations, a sample size which for most raptors can hardly be obtained within several months (see Results). Probability of detecting a bird could not be estimated. Hence any technique based on such an estimation (Cochran 1977) could not be used. Individuals were not distinguishable and time was too short to make repeated counts on most transects, thus preventing another method for estimating probability of detection (Seber 1982) to be used. My survey was not devised to calculate proportion of the area occupied (Geissler and Fuller 1986), a promising technique especially if birds are detected by responses to playbacks of their calls.

Therefore, the alternative method used was a strip transect census which gave the best compromise between efficiency and biases (Burnham et al. 1985; Verner 1985) and used the traditional concepts of detectability and effective area surveyed (Emlen 1971; Ramsey and Scott 1981). Strip transect census is equivalent to a long narrow quadrat within which all birds are assumed to be recorded. The transect was unbounded, drawn randomly, and transect width was not adjusted to varying density of vegetation which changed constantly but within rather narrow limits at mid- or upper-levels. Daily sections covered were of unequal size and many were traced 2 or more different d . There is a distance from the observer under which the species studied almost always

move, fly or call and thus can be detected. Large terrestrial game birds and macaws (*Crax*, *Psophia*, *Ara* spp.) were also included in the survey and were almost always first detected by calls. Flushing or detection distance is a critical parameter which has proved, from my experience in Guiana, to be rather constant for a given species in primary, not hunted, forest. Detection distance is also lower than maximum distance (both vertically and horizontally) at which birds are visible in undergrowth of high primary forest, ensuring that most birds do not flee when out of sight. Any departure from basic assumptions leads to an underestimation of density.

Such specific detection distance (d) is used here as the radius of a circle moving with the observer at its center and whose dia is the effective minimum width of the strip transect. Sighting angle or perpendicular distance are no longer involved since birds become conspicuous in any quarter as soon as the observer is closer than d . Then density estimate is

$$\hat{D} = n/2dL$$

where n is the number of birds detected within the $2d$ -wide strip and L is the length of the transect.

From all individual detection distances obtained, d will be the shortest distance at, or interval within which the largest number of birds were recorded [i.e., width maximizing the density estimate (highest n/d ratio)]. Thus, detections further than d are not used. Sampling variance of the density estimate is dependent on sampling variance of n which could be estimated from replicated counts. However, sample size was so small that the variance was inevitably large and not very meaningful.

Data Collection on Strip Transect. Field counting procedure, or search method, was carefully devised to meet as much as possible the prerequisite assumptions of the strip census (all objects must be detected within the limits and have a fixed initial position; all sightings must be independent events and their distance must be accurately measured). I walked very slowly (<1 km/hr), making as little noise and movement as possible, along narrow trails or through undisturbed undergrowth and randomly crossing every forest type. Attention was focused exclusively on raptors and large game birds (*Crax*, *Psophia*, *Ara*). Only periods between sunrise and sunset, without rain, fog or strong wind, were taken into account.

I recorded every bird either sitting, walking or

flying, from ground level to top of the canopy, but not above. Distances between the observer and first sighting were measured with a range finder (Opti-meter 620) then controlled with the number of steps and rounded to the upper 5 m-interval. Although not used subsequently, angle deviation from the transect was read through the sighting mirror of a liquid filled compass. For each observation I also recorded the number of individuals, their age, sex, height, behavior, location on the map, direction of flight, as well as habitat type and vertical structure of the vegetation (estimated index of density, ranked from 1-4 in the 0-2, 3-14, 15-25, 26-36 and >36 m strata).

Birds were often detected when taking flight or alighting. Those calling were recorded only if they were within sight distance. Only Caracaras, which almost always utter their loud alarm calls when seeing an observer, were sometimes noted further away, but never at more than 100 m. Some birds were seen in or from a tree-fall gap and their detection distance may have been higher than in closed understory. Transect length was measured daily on a 1/50 000 scale map and monitored using a pedometer. Total distance walked in good censusing conditions through the 100 km² study area in 1986-1987 was 517 km in 498 hr.

Similar censuses were performed from 1981-1986 in 8 other study areas throughout French Guiana (total: 1188 km in 1135 hr). Being often associated with the survey of other species, these censuses could not be as accurate (uneven speed, attention distracted) and results may sometimes underestimate raptor densities.

Additional Techniques. Other methods are promising for application to the most secretive species but are time consuming with limited results (Thiollay and Tostain unpubl. data), as far as population estimate over a large area is concerned.

Trapping and marking. Forest Falcons and Bicolored Hawk are not infrequently caught in mist nets or traps baited with live birds, but few other species have been caught in this way. Yet, only an unknown fraction of the population is likely to be captured, which does not fit our purpose. Subsequent radiotracking of tagged birds has proved to be invaluable to assess home range and foraging patterns of individual species but can hardly be considered for a relatively short period multispecies survey. Radiotracking could also be an elegant method to find occupied nests. Sightings and recaptures are so

rare that visual marking and banding are of limited interest for secretive species.

Vocalisations. Fortunately, several species have loud calls which helps in detection and location. First of all, the very noisy groups of Red-throated Caracara and Black Caracara (*Daptrius ater*) are easy to follow and cannot be missed if one moves a few hours through their home range. Around their nest, the Orange-breasted Falcon and Bat Falcon (*Falco rufi-gularis*) are aggressive and vocal even when not breeding but may be silent and unobtrusive a few hundred meters away. Black and the Ornate Hawk Eagles, as well as, to a lesser extent, the Great Black Hawk, rarely fail to perform display flights above canopy with loud calling nearly every day if the weather is fine, but usually during a short time (5-15 min) and only once-a-day in mid- or late-morning. Thus, territorial pairs can be located from inside the forest.

The 4 sympatric Forest Falcons (*Micrastur rufi-collis*, *M. gilvicollis*, *M. mirandollii* and *M. semitorquatus*) are all very vocal but mainly during a short time at dawn when it is usually too dark to see them in the understory. Most stop calling before sunrise and in Guiana during the dry season only *M. mirandollii* and *M. semitorquatus* are likely to be heard with some frequency later in the morning and around sunset. However, calls (which are probably true songs) are quite variable, rather similar to each other and not always easy to determine. Unfortunately, playback experiments conducted so far rarely elicited a response (outside the dawn chorus) and failed to attract birds. Many more attempts are still necessary to define which part of their call repertoire may be most efficiently broadcasted, at what time and at what distance. Population density of the 6 km² central zone has been drawn from distribution of calling birds, assuming that both sexes were vocal (often 2 birds close to each other seemed to call in turn or together).

Other techniques such as audio-luring utilizing prey calls are being developed in the northern Neotropics and have already produced some very promising results (J. Vannini, pers. comm.). Playback of conspecific calls to attract birds or elicit a vocal response is certainly worth additional study although some species may not be lured. Flushing canopy birds or searching for nests using a low flying helicopter has been attempted repeatedly in French Guiana with disappointing results. Specific trapping methods also remain to be investigated.

RESULTS

I am only concerned here with applicability of census methods actually used. More details about densities and distribution patterns are given elsewhere (Thiollay 1989).

Understory Mapping. The Red-throated Caracara alone provided enough records to construct comprehensive home ranges, not only from >200 sightings but from the movements of noisy flocks followed out of sight and the location of roosting places (Fig. 2). Limits between group territories have been checked by simultaneous records of contiguous flocks. Outside the 6 km^2 intensively surveyed core area, all other species were seen or heard too infrequently to accurately map territories, and no individual was marked. Nevertheless, data were useful in assessing overall distribution of non-soaring species and to check from the ground the exact location of birds displaying over the canopy far from any lookout.

Strip Census. Notwithstanding the low number of records on strip transects, density estimates obtained on strip census through the 100 km^2 study area are remarkably close to those derived from mapping of soaring birds on the restricted 42 km^2 -circle. The 2 estimates are within a range of $\pm 40\%$ for 6 of the 8 species available for comparison (Table 1). Significantly, lower densities are given by strip census for species either very shy, secretive and unevenly distributed (*A. bicolor*) or restricted to tree tops and openings (*L. albicollis*). At least 2 pairs of Lined Forest Falcon (*Micrastur gilvicollis*) were found on 300 ha in the Central zone; the strip census slightly underestimates the overall density of this secretive species.

The Red-throated Caracara, according to our results, is the most abundant raptor. On the study area the Caracara lives in flocks of 4–7 birds. Mean number of individuals recorded per flock encounter on the $\leq 200 \text{ m}$ wide strip transect (3.43 ± 0.91) is lower than actual size of groups occurring on the study area (5.50 ± 0.90 , $N = 12$). Yet overall density obtained by the strip census method is markedly higher than that derived by plotting the flock home ranges (Table 1 and Fig. 2). Frequency and length of the Caracaras' movements violate the basic as-

sumption underlying computation of density using the strip method and probably leads to the overestimation found here.

Mean Density of Aerial Hunters. Raptors hunting over the canopy are usually seen on line transects only in flight and where the canopy is rather open. Such records would violate the main assumptions of the strip census method and thus cannot be used except to map species distribution. Mean number of individuals seen per hour over a given area has a high variance and can rarely be extrapolated to a much larger area. Only instantaneous densities would be reliable but are feasible only if almost all birds are in flight at the same time over a large area. This assumption is met only for vultures during the best hours and it has been used as a minimum estimate of the total population (Table 2). Kites, on the other hand, are not on the wing for such long and predictable periods. Therefore, the basic estimate of mean number of birds seen in flight over a given area may be biased and must be complemented by maximum flock size and the localisation of pairs.

Mapping of Soaring Birds. Mapping is by far the easiest and probably the most accurate technique when suitable lookouts are available (Fig. 3). However, any method relying on occurrence of raptors soaring over the forest is very sensitive to activity pattern of the species involved. Detectability of most forest species may be very low, even when the observer overlooks the whole territory of a pair in fine weather. The probability to contact a species at least once during any 1-hr observation bout is $<50\%$ for 10 of 14 species and $\leq 30\%$ outside the 0900–1200 H period (Table 3). There is $>85\%$ chance of encounter only for 2 species and during the midday period. At the other extreme, 5 of 14 species have been recorded in $<15\%$ of any hour.

If one takes into account the actual time spent in flight, 11 of 14 species are visible $<5\%$ of the daylight period whereas the 2 most conspicuous (*Cathartes* and *Ictinia*) were seen an overall 14–16% of the time. From mid-morning to mid-afternoon (peak of activity), the last 2 species were visible during 20–25% of the time against $<10\%$ for all others and even $<1\%$ for 5 species.

It is not known how the time budget of these

Figure 2. Distribution of groups of Red-throated Caracaras (*Daptrius americanus*) over the 100 km^2 study area. Dashed lines: see Figure 3. Open limits: uncertain boundaries due to lack of records because of an insufficient survey in marginal areas.

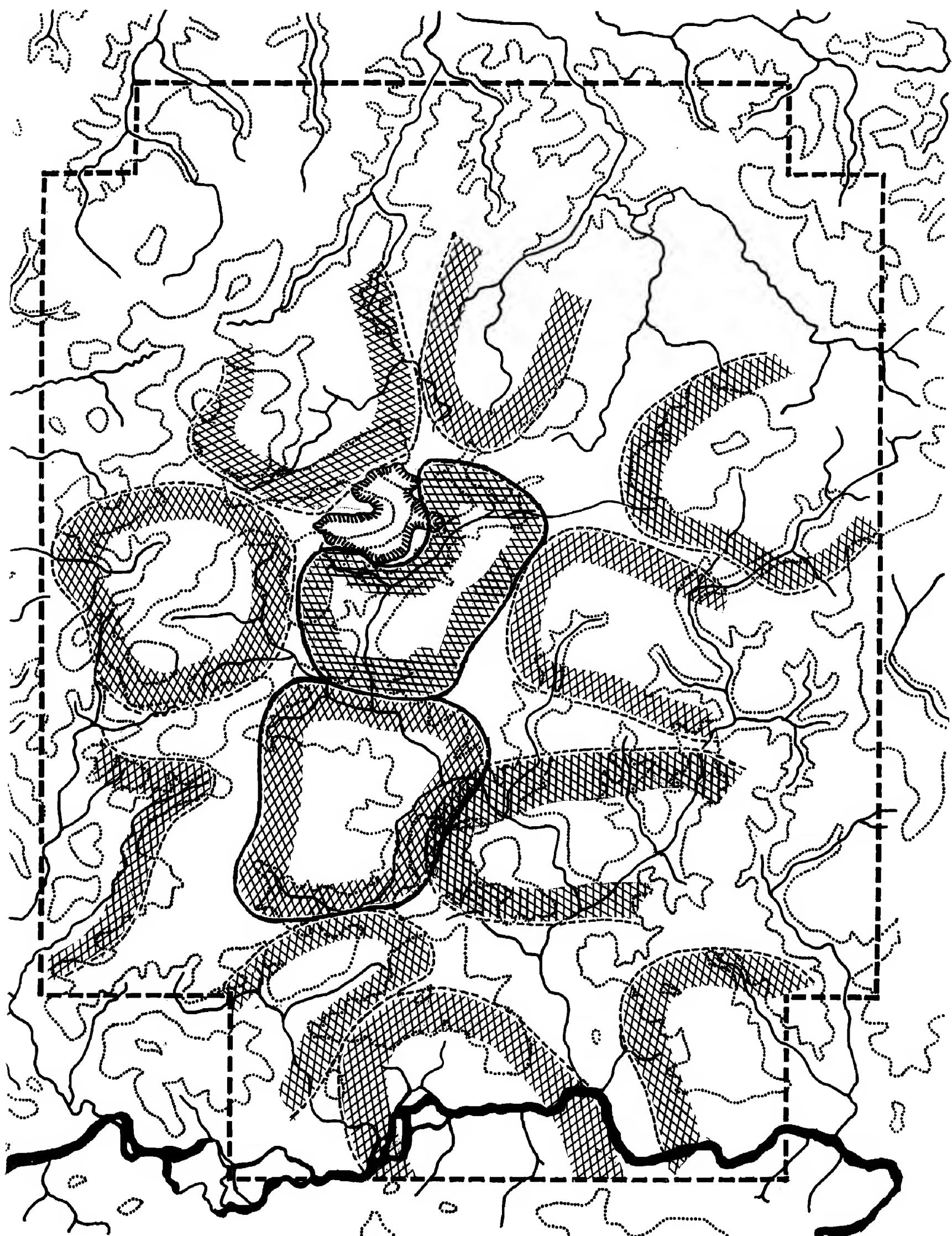


Table 1. Comparative results of quantitative surveys of territorial raptors in primary rain forests of French Guiana. **Zone I:** intensive soaring bird census and understory mapping on 6 km² (see text). **Zone II:** mapping of soaring birds on 42 km². Total area: minimum population estimate, combining both methods, on the 100 km² study area. Data are numbers of individuals (i.e., ≥ 2 times the number of pairs). Strip censuses: N = number of birds recorded within 100 m on either side of cumulative line transects (517 km for the main study area and 1188 km for other localities). d = detection distance (m) maximizing the density estimate \hat{D} (in number of individuals/100 km²).

SPECIES ^a	MAIN STUDY SITE						8 OTHER LOCALITIES		
	ZONE I	ZONE II	TOTAL AREA	STRIP CENSUS			STRIP CENSUS		
				N	d	\hat{D}	N	d	\hat{D}
<i>Leptodon cayanensis</i>	0	0	≥ 2	1	30	3.2	1	25	1.7
<i>Harpagus diodon</i>	≤ 1	± 2	≥ 2	1	25	3.9	2	25	3.4
<i>Harpagus bidentatus</i>	≤ 2	± 6	> 8	3	20	14.5	9	25	15.1
<i>Accipiter bicolor</i>	≤ 2	± 4	≥ 6	1	25	3.9	2	20	4.2
<i>Leucopternis melanops</i>	≤ 2	—	≥ 2	1	25	3.9	8	30	11.2
<i>Leucopternis albicollis</i>	± 3	± 10	15	5	50	9.7	10	35	12.0
<i>Buteogallus urubitinga</i>	± 3	≤ 12	≤ 20	10	45	17.2	9	40	9.5
<i>Morphnus guianensis</i>	≤ 1	2	≥ 2	2	40	4.8	3	35	3.6
<i>Spizastur melanoleucus</i>	< 2	< 4	≥ 6	3	30	6.4	5	30	7.0
<i>Spizaetus ornatus</i>	< 2	4	≤ 10	9	45	12.9	15	50	10.1
<i>Micrastur semitorquatus</i>	≤ 2	—	≥ 10	3	25	11.6	10	25	13.4
<i>Micrastur ruficollis</i>	≤ 2	—	> 8	2	20	9.7	3	20	6.3
<i>Micrastur gilvicollis</i>	≥ 4	—	> 30	22	20	72.5	31	20	63.0
<i>Micrastur mirandollei</i>	≤ 2	—	≥ 6	1	25	3.9	4	25	5.0
<i>Daptrius americanus</i>	± 6	—	≥ 66	206	100	199.2	395	100	166.2

^a Additional species: *Accipiter superciliosus*, *A. poliogaster*, and *Spizaetus tyrannus* (one pair of each recorded on the main study area) and *Harpia harpyja* (3 records, only outside the main study area, $\hat{D} = 3.1$).

Table 2. Population estimate of vultures and kites hunting in flight above the canopy. Number of individuals crossing a 10 km² sample area (mean of 20 hr between 0900 and 1200 H); number of territorial pairs or families settled within the 100 km² study area; highest number of birds seen together; total population (i.e., resident adults + fledged young + estimated additional birds).

	MEAN NUMBER		NUMBER OF RESIDENT PAIRS LOCATED/100 KM ²	HIGHEST CONCENTRATION RECORDED	AVERAGE POPULATION (IND/100 KM ²)
	OF	BIRDS/HR/10 KM ²			
	\pm S.D.				
<i>Cathartes melambrotus</i>	1.95 \pm 1.50		?	12	19
<i>Sarcoramphus papa</i>	0.90 \pm 0.96		2	7	9
<i>Elanoides forficatus</i>	0.60 \pm 1.09		2	30	≥ 10
<i>Ictinia plumbea</i>	1.90 \pm 0.97		3	7	9

Figure 3. Distribution of territorial pairs of the Great Black Hawk (*Buteogallus urubitinga*) over the 100 km² study area of primary rain forest. Home ranges shown here are mostly areas covered by displaying adults. Dashed lines are provisional limits based on too small a number of records or on observations that could not be accurately located.

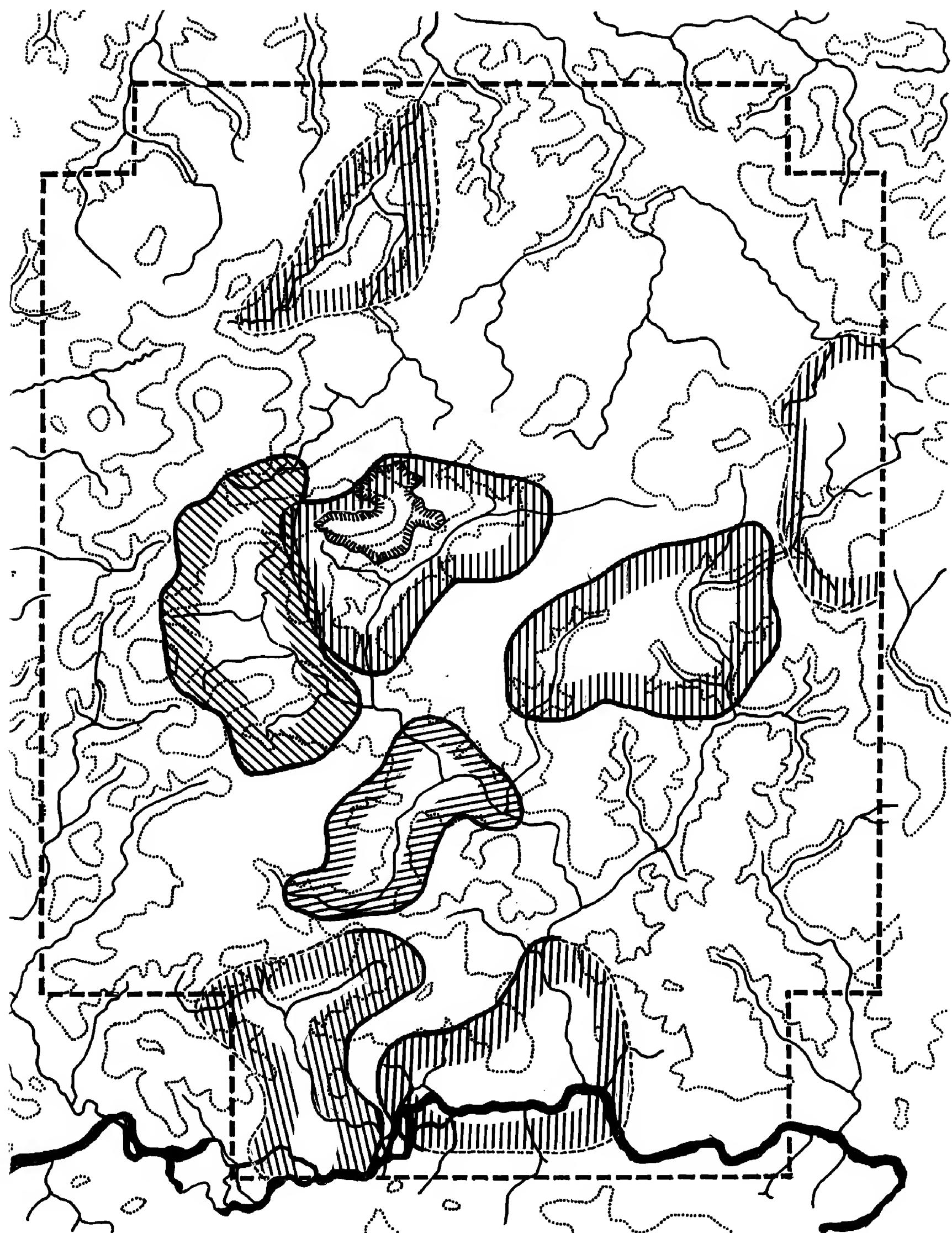


Table 3. Occurrence of soaring raptors over a 10 km²-area of primary forest. Proportion of time 1 or more birds spent in flight, then probability to record the species during 1 hr and number of birds counted within each hour. Observation periods: A = 0630–0900 H; B = 0900–1130 H; C = 1130–1530 H; D = 1530–1800 H. Sample sizes (hours): A = 17; B = 20; C = 17; D = 17.

SPECIES	PERCENT OF OBSERVATION TIME WHERE ≥ 1 BIRD WAS FLYING OVER THE FOREST				PERCENT OF 1-HR PERIODS WHERE THE SPECIES WAS RECORDED				MINIMUM NUMBER OF INDIVIDUALS SEEN/HR (RANGE)			
	A	B	C	D	A	B	C	D	A	B	C	D
<i>Cathartes melambrotus</i>	1.3	27.9	22.1	5.1	18	85	100	47	1–2	1–6	1–6	1–5
<i>Sarcoramphus papa</i>	0.7	12.3	4.5	2.1	6	55	24	30	1	1–3	1–2	1–2
<i>Elanoides forficatus</i>	5.9	5.5	6.5	10.6	24	30	30	30	1–7	1–3	1–15	1–17
<i>Harpagus diodon</i>	—	0.7	0.9	—	—	5	6	—	—	1	1	—
<i>Harpagus bidentatus</i>	1.0	3.3	—	—	12	40	—	—	1	1–3	—	—
<i>Ictinia plumbea</i>	9.5	22.8	17.1	17.2	47	100	77	71	1–4	1–4	1–3	1–7
<i>Accipiter superciliosus</i>	—	0.3	—	—	—	5	—	—	—	1	—	—
<i>Accipiter bicolor</i>	—	0.9	—	—	—	10	—	—	—	1	—	—
<i>Leucopternis albicollis</i>	0.1	7.7	0.2	—	6	45	6	—	1	1–4	1	—
<i>Buteogallus urubitinga</i>	0.7	9.2	4.5	0.1	41	75	47	6	1–2	1–4	1–2	1
<i>Morphnus guianensis</i>	—	1.3	—	—	—	15	—	—	—	1	—	—
<i>Spizastur melanoleucus</i>	0.4	0.8	—	1.8	12	10	—	12	1	1	—	1
<i>Spizaetus ornatus</i>	—	3.6	0.6	—	—	25	6	—	—	1–2	1	—
<i>Falco deiroleucus</i>	1.3	4.3	1.6	5.1	30	50	24	24	1–2	1–2	1–2	1–2

species, and hence their detectability, may vary over the seasons. Obviously, long periods of time with good observational and weather conditions are necessary to assess the presence of some species, let alone their spatial distribution. However, several very territorial species (*H. bidentatus*, *B. urubitinga*, the 2 *Spizaetus* and, to a lesser extent, *L. albicollis* and *Spizastur*) performed their display flight once nearly every day, mostly in late morning when soaring conditions were suitable. Displays often lasted 5–15 min but proved to be a fairly reliable indication of an occupied territory. Thus, concentrating most research during the favorable hours may save much time and, for such species, most information may be obtained within only 1–2 d. Conversely, to assess confidently the presence or absence of the most secretive species (*H. diodon* and *Accipiter* sp.), which are more occasionally soaring, it is necessary to repeat the above observation from a vantage point for at least 6–7 d. (Table 3). Indeed, a complete mapping of their territory may require much more time.

DISCUSSION

Reliability of results rests with the detectability of each species. Therefore, specific behavioral traits

determine the most appropriate census methods (Table 4).

Mapping of soaring birds was the most accurate technique. Territorial species regularly displayed above the canopy and easily provided a fairly convenient set of data within a rather short time. For many pairs, almost no additional information was accumulated after 2–3 d of fine weather. However, most territory sizes may be very conservative estimates because of potential biases: 1) some species (e.g., *Accipiter*) perform relatively short flights and may not display over their entire home range; 2) it is not known whether the area flown coincides with defended territory and/or hunting range; 3) a few exceptional flight circuits of individuals not surely identified, or long pursuits of a neighbor, were ignored; 4) the exact position of birds too far away was not precise and always conservatively estimated. There was a substantial floating population, either transient birds or members of temporary or permanent trios.

Conversely, an accurate mapping of non-soaring species is difficult without the help of time consuming radio-tracking. First of all, unmarked birds cannot be assigned to a particular pair or territory. More

Table 4. Behavior and most suitable census methods of forest raptors in French Guiana. MS = mapping movements of soaring territorial pairs; TP = minimum estimate of total population. Extrapolation of the mean number of individuals soaring over a given area; MU = mapping location and movements of birds seen or heard in the understory; DE = mean density estimate from understory strip census.

BEHAVIOR	SPECIES	METHODS			
		MS	TP	MU	DE
Soaring—regular:					
Mid-late morning; loud calls rarely heard	<i>Buteogallus, Spizaetus</i>	+		+	+
	<i>Leucopternis albicollis</i>	+			
	<i>Harpagus bidentatus</i>	+		+	+
Mid-morning to mid-afternoon	<i>Cathartes melambrotus</i>		+		
	<i>Sarcoramphus papa</i>	+	+		
Morning to evening	<i>Elanoides forficatus</i>	+	+		
	<i>Ictinia plumbea</i>	+			
	<i>Falco</i> (2 sp)	+			
Soaring—Occasional:					
Mid-late morning	<i>Leptodon, Morphnus</i>	+		+	+
Morning and afternoon	<i>Accipiter, H. diodon,</i> <i>Spizastur</i>	+		+	+
Non-soaring—silent:					
Sometimes conspicuous secretive (undergrowth)	<i>Harpia harpyja</i>			+	+
	<i>Leucopternis melanops</i>			+	+
Non-soaring—calling:					
Early morning	<i>Micrastur</i> (4 sp)				+
All day	<i>Daptrius</i> (2 sp)				+

importantly, frequency of encounters with secretive and/or rare species is extremely low. Even the Lined Forest Falcon, by far our most common solitary raptor, was sighted at best once every 2 or 3 d, whereas most other species were spotted as a mean only once every 13–56 full d (>10 hr/d) spent actively searching the forest. Only species often flying low over the canopy (kites, vultures, *Buteogallus*, *Leucopternis*, *Spizaetus*) were seen once every 3–10 d. I met with 1–3 groups of Caracaras nearly each day along a 10 or more km line transect. A low rate of raptor encounters seems to be more a consequence of very low density, uneven distribution or too confiding a behavior rather than of shyness, since some perched birds allowed a surprisingly close approach or did not take flight when they were in the upper canopy. The possibility that some species or pairs may be overlooked is suggested by the following examples. *Accipiter poliogaster* was identified here for the first time in French Guiana even though 10 other similar areas had been carefully surveyed in previous years. A pair of *Chondrohierax uncinatus* was found breed-

ing in March 1989 in the study area where it was never seen before.

The strip census method, or any technique adapted from it to the conditions of the rain forest, remains to be encouraged, provided that underlying assumptions are carefully respected. Good results have been obtained with large terrestrial birds [the Trumpeter (*Psophia crepitans*) and the Curassow (*Crax alector*)]. Each lives in small flocks, slowly moving in the undergrowth and always giving a soft alarm call without fleeing, allowing the observer to detect their presence.

The overall consequence of possible biases is an underestimation of the density of most species, especially when large areas (>10 km²) and small species are involved. The density estimate of the 100 km² area is lower than that of the intensively surveyed 6 km² core area for 11 of 14 species (Table 1). However, the greatest care must be taken in extrapolating density of a small area to a larger area, because many species are patchily distributed and territories are far from being contiguous. An overall

density estimate is meaningful only if drawn from an area including >2 pairs. Such an area is necessarily large for most species and difficult to survey.

CONCLUSION

To obtain a reliable density estimate of breeding raptors in a primary rain forest, the best strategy should be the design of a particular census method for almost each species separately (i.e., a specific mixture of several techniques complementing each other). Moreover, following radio-tagged birds should be strongly encouraged and is currently the only way to confirm the actual territory size of most species.

When the aim is only to compare the raptor population of different forest areas, it may be advisable to use a specific abundance index. Such an index may be the highest frequency (e.g., mean number of individuals recorded/hour) given by the most rewarding method for the species involved. Indeed, any index is comparable within but not between species. The same technique should be used for a given species over different study sites (including season, time of day and sighting radius). So, the method would avoid the biases of density estimates coming from different specific detectabilities and the more difficult assessment of actual density.

Time is more accurately and easily measured than area or distance and is a more constant unit. I have found here better correlations between number of birds detected and time spent than with distance travelled (all specific $r = 0.68-0.92$; $P < 0.01$), either inside or outside the forest.

Results are encouraging but we are far from mastering reasonably easy and accurate census methods appropriate for most raptor species within large areas of dense rain forest. Always necessary will be the use of several censusing methodologies in conjunction, including audio-luring, in order to minimize biases inherent in all. To work out and test such methodologies remains an urgent challenge with regard to rapidly declining tropical forest raptors.

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NATURAL HISTORY OF THE AMERICAN KESTREL IN VENEZUELA

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ABSTRACT.—American Kestrel (*Falco sparverius* L.) populations in southwestern Venezuela achieve highest densities in transitional areas, including deforested ranch lands, grasslands and villages. Field observations focused on pair formation, copulation, territorial defense, production feeding, predation, caching and nesting success. Collected specimens provided information on molt, brood patches, reproductive condition and general morphometrics. Breeding biology and natural history of 22 pairs compared closely with North American populations. Kestrels breeding in Venezuela are smaller than North American individuals, but percent size difference between the sexes is similar in both Americas. South American pairs inhabited small territories, harvested small prey, invested heavily in defense and produced few to no young.

American Kestrel (*Falco sparverius* L.) populations span North, Central and South America from tree line areas of Alaska to open fields of southern Chile (see Brown and Amadon 1968; Cade 1982). There are, however, no published accounts of the biology of kestrels from tropical mainland areas.

This study includes general field observations of kestrels from central to western Venezuela with a detailed natural history of a population in the west. Eleven pairs which resided at El Bayuelo and 11 other pairs from surrounding areas were included in this study. Specific aspects of the biology of kestrels in California and Venezuela were compared.

STUDY AREA AND METHODS

From December 1982 into May 1983 kestrels were studied in central and western Venezuela, including the states of Tachira, Merida, Trujillo, Barinas, Zulia, and Apure. Near Coloncito (Lat./Long. 8°2'N, 72°16'W) in the State of Tachira, a local population of kestrels inhabiting the Hacienda El Bayuelo (Fig. 1) was studied in detail. The 720 ha hacienda is located 9 km north of Coloncito at the foot (30 m elev) of the northwest slope of the Andes. Prior to construction of the Pan American Highway, the area around Coloncito was jungle. In the intervening years virtually all jungle vegetation was cleared for cattle ranching, and only a few small tracts and waterways (canos) remain. Rio Jabillo enters the property from the east. Observations in the field totaled 700 hr.

As part of intensive land management associated with cattle ranching, pastures are tilled every 3–4 mo and replanted by hand with cuttings of Aleman grass which delays natural succession and fortuitously provides habitat for kestrels. Factors promoting kestrel habitation, prey, perches, nest cavities and open vegetation are available in ranching locations.

A dry season from August–September to March–April and a wet season from April–May to July–August characterize weather patterns at the hacienda. High humidity

with fluctuating temp. (mid 20°–mid 30°C) was typical. Approximately 12 hr of sunlight occur daily.

RESULTS

Kestrels inhabited desert and desert scrub of Barquisemento, high cactus deserts of Estanquez (Merida), and open llanos to the east and west of Cordillera de Los Andes. Birds infrequently inhabited the paramos, jungles, riparian zones (Rio Chama near Merida, Rio Mucuiepe of Zulia), and cloud forests to the north and east of Mericay. Cities of Merida, Valencia, and San Cristobol also supported breeding pairs. Highest numbers of kestrels however, occurred in natural or man-created transitional areas between forests and plains, in villages, agricultural fields, cattle ranches and jungles. Breeding kestrels were found from coastal scapes of Moron to over 2440 m where epiphytes grow red in El Valle. Kestrels have been recorded up to 3000 m (De Schauensee and Phelps 1978).

Morphometric Measurements of Kestrels. Thirty-six kestrels (19 ♂♂, 17 ♀♀) were collected for morphometric study. Wing, tail and tarsi length did not significantly differ between sexes (Table 1). Intra- and inter-sexual comparisons between weights of kestrels in North (NA) and South America (SA) showed a significant difference by sex and area (Table 1). Overall, kestrels in South America are generally smaller. Both populations show a similar percent size difference between the sexes (NA = 88.1%, N = 42 ♂♂, 45 ♀♀; SA = 87.9%, N = 17 ♂♂, 12 ♀♀, see also Table 1).

Of the 36 collected specimens, 12 individuals represented 6 breeding pairs (Table 2). Individuals in molt were observed from December to May. During

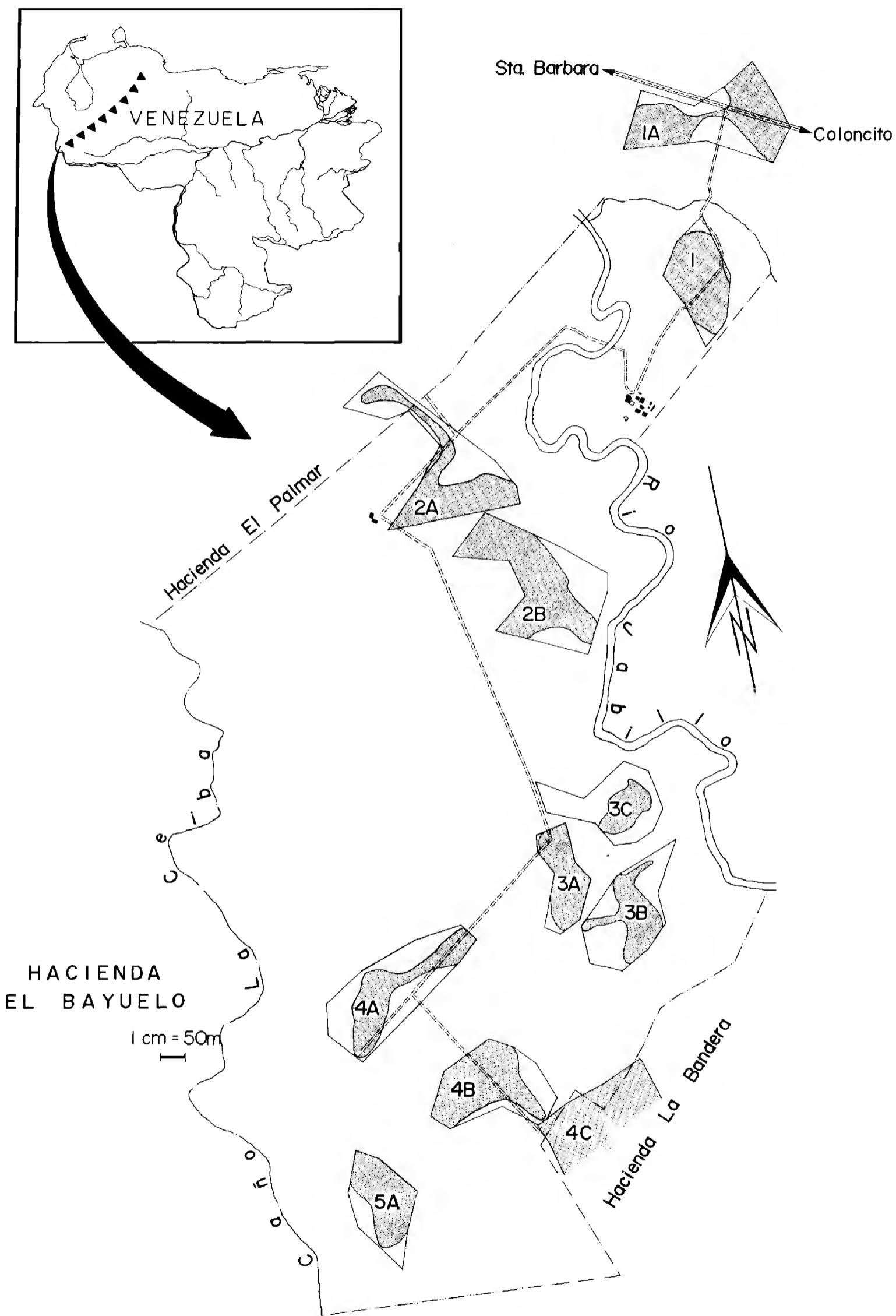


Table 1. Student's *t*-Test comparisons of morphometric measurements of the sexes of American Kestrels in Venezuela and between Venezuelan and North American kestrel populations.

	♂				♀			
	\bar{x}	S.D.	N	P	\bar{x}	S.D.	N	P
Venezuela								
Weight (g)	95.0	7.6	17		108.1	6.2	12	<0.001
Wing (mm)	181.5	6.5	19		185.4	11.3	17	NS
Tail (mm)	130.1	6.6	19		132.9	12.1	17	NS
Tarsus (mm)	38.8	2.0	19		39.1	1.9	17	NS
North America								
Weight (g)	103.7	13.5	42	<0.001	117.7	17.7	45	<0.05

this period, males showed less molting in flight feathers than females (Table 2). In both sexes brood patches formed early in the breeding cycle; at least several weeks before eggs were laid. In two females brood patches had formed before the ova had begun to enlarge (SJSU-MBM #6033) or fully develop (SJSU-MBM #6037). Their mates (SJSU-MBM #6044 and SJSU-MBM #6065) had formed brood patches slightly later. One female (SJSU-MBM #6041) however, failed to produce eggs or a brood patch, while her mate of several months (SJSU-MBM #6039) possessed enlarged gonads and slightly developed brood patches. Brood patches began to involute late in the breeding cycle (April–May).

Breeding Biology. Kestrels in Venezuela occupy and defend territories (Fig. 1) in December and January, but by February pairs are established. Kestrel territories at El Bayuelo averaged 12.2 ha (S.D. = 4.4; N = 10) in size (see Table 3). Not all pairs however, breed, and 3 of 11 pairs remained in the courtship phase for at least 22 wk. One pair at El Bayuelo associated for 3 mo but failed to form brood patches or produce eggs.

Early in pair formation, kestrels occupied extensive areas, including all or part of an eventual territory. Exposure on high perches, mutual avoidance, vocalizations and defense were associated with a territory. Active defense included "klee" vocalizations (Willoughby and Cade 1967), attacks with pendulum dives (Balgooyen 1976) or chases which were

direct or undulating in pattern. Interspecific behavioral encounters of kestrels involved 29 species, 17 of which were raptors (58.6%) and 8 species (27.6%) represented food competitors (Table 4). No response was recorded for 22.2% of the encounters. Interactions with raptors accounted for 90.0% of pair response time. Sexes did not differ statistically in number of encounters. However, males appeared to react longer and with more vigor than females when both responded to encroachment.

Copulation. Copulations were observed anytime from 2 January in Barinas to 17 April at El Bayuelo. Of 95 copulation attempts 57% (N = 54) were identified as to which sex initiated copulation. Females initiated copulation 41% of the time by moving toward their mate, or by posturing (Balgooyen 1976).

Incomplete copulations (no cloacal contact) occurred in 14 of 54 attempts. Females held their tails to the left during copulation 63.5% (N = 66) of the time. Mean duration of 74 complete attempts was 6.7 s (S.D. = 2.7 s). Chitter, whine, and whine-chitter vocalizations (Willoughby and Cade 1967) were given during copulation. At El Bayuelo males more frequently chattered and females were more likely to whine. High intensity chittering by males was associated with thrusting. In general vocalizations of any kind throughout the season were infrequent and brief in duration.

Prey Transfer. Food provisioning by males is an integral part of pair formation and maintenance and

Figure 1. Breeding territories of American Kestrels at hacienda El Bayuelo, Venezuela. Areas of high occupancy are shaded within defended borders. Territories were determined by noting kestrel perches and sites of defense which were plotted on a map (scale 1:5000). A compensating polar planimeter measured the maximum area of territorial polygons. (Darts represent the Andes Mountains.)

Table 2. Reproductive characteristics of 6 breeding pairs of kestrels in the States of Tachira, Zulia, and Apure, Venezuela.

STATE	PAIRS	DATE COL- LECTED	WEIGHT (G)	MOLT	BROOD PATCHES (MM)	TESTES L (MM) R (MM)	OVARY
Tachira	♂ 34	31 Mar	100	none	small 13 x 9	6.5 x 5.0 4.0 x 4.0	3 ova; small (1 week of prod. feeding)
	♀ 35		116	P #6 L/R in quill	none		
Tachira	♂ 30	17 Mar	100	4th primary L/R new		6.0 x 3.0 5.5 x 2.5	3 corpora lutei (3 young)
	♀ 31		105	tail	19 x 25		
Tachira	♂ 44	8 Apr	101	none		3.5 x 3.0 3.0 x 2.0	2 corpora lutei (2 females fledged: female 46 = 103 g female 47 = 124 g)
	♀ 45		109	none	35 x 20		
Tachira	♂ 54	16 Apr	105	none	none	7.0 x 4.0 6.0 x 3.5	
	♀	Not coll.					
Zulia	♂ 56	15 Apr	98	slight body molt	regress: 28 x 30	(small) 2.5 x 3.0 1.5 x 1.0	2 corpora lutei
	♀ 55		106	4th R/L primary	29 x 20		
Apure	♂ 9	12 Feb	88	none	new, incomplete	6.5 x 4.0 4.5 x 2.5	4 ova, fat deposits, 6.5 mm to 11.5 mm
	♀ 10		118	5 pri. new L/R	35 x 27		
Apure	♂ 16	12 Feb	87	none	starting	5.0 x 3.5 4.0 x 2.5	not developed
	♀ 15		96	4 pri. new 5 in quill	3 x 18		

Table 3. Size of defended territories for several American Kestrel populations.

LOCALITY	AREA (KM ²)	N	REFERENCE
E. Bayuelo, S.A.	0.12	10	Balgooyen (this study)
Quebec	0.24	20	Bowman and Bird (1986)
Jamaica	0.44	6	Cruz (1976)
Utah	0.67	12	Smith et al. (1972)
California	1.20	43	Balgooyen (1976)
Illinois	5.06	4	
Wyoming	5.06	22	Enderson (1960)
Michigan	5.86	—	Craighead and Craighead (1956)
\bar{x}	2.33		

could provide energy for egg production (see Balgooyen 1976; Coonan 1984). As the female becomes more sedentary and foregoes hunting, an active period of "production feeding" begins by the male.

Prey transfers among pairs at El Bayuelo began in late January. By frequency insects and lizards constituted 97.6% of the transferred prey; insects alone comprised 50.8% (Table 5). Two non-producing pairs at the hacienda continued production feeding for more than 4 mo. The time of transition to extensive male provisioning ranges from 1 or 2 d to several days or weeks for most pairs, and occurred a few weeks before eggs were laid.

Observations of successful breeding pairs showed a bias of augmented lizard consumption in female diet. Females captured lizards at a percent biomass

Table 4. Encounters of American Kestrels at El Bayuelo, Venezuela

SPECIES	BEHAVIORS										DISPLAY ³			
	ENCOUNTERS		RESPONSE TIME		SEX		CALLS ²			DISPLAY ³				
	(R) ¹	(NR)	(SEC.)	MEAN	♀	♂	S	K	C	D	P	R	C	W
RaptoRs														
Black Vulture (<i>Coragyps atratus</i>)	4	3	25	6.2	2	4							3	1
Turkey Vulture (<i>Cathartes aura</i>)	13	10	120	9.2	7	9							11	2
Black-shouldered Kite (<i>Elanus caeruleus</i>)	2	1	25	12.5	1	2							2	
Pearl Kite (<i>Gampsonyx swainsonii</i>)														
Swallow-tailed Kite (<i>Elanoides forficatus</i>)	1		5		1									
Snail Kite (<i>Rostrhamus sociabilis</i>)														
Roadside Hawk (<i>Buteo magnirostris</i>)	17	1	755	44.4	7	12	10	6	1	3	12	2		
Gray Hawk (<i>Buteo nitidus</i>)	4		1010	252.5	1	4					4	1		
Savanna Hawk (<i>Heterospizias meridionalis</i>)	19	1	1355	71.3	11	17	9	10		2	17			
Common Black Hawk (<i>Buteogallus anthracinus</i>)	2		25	12.5	1	1								
Laughing Falcon (<i>Herpetotheres cachinnans</i>)	1		70		1	1					1			
Barred Forest-Falcon (<i>Micrastur ruficollis</i>)	1		360		1						1			
Yellow-headed Caracara (<i>Milvago chimachima</i>)	15	5	225	15.0	7	15	9	1						
Crested Caracara (<i>Polyborus plancus</i>)	13	6	60	4.6	8	8	4	2	13					
Bat Falcon (<i>Falcon rufigularis</i>)	1		150		1	1					1			
Applomado Falcon (<i>Falco femoralis</i>)	4		605	151.2	2	3								
American Kestrel	12	5	145	12.1	12	14								
N = 109		35	4935		66	91								
% Total = 68.6		77.8	90.0		73.0	74.0								
Non-RaptoRs														
Cattle Egret (<i>Bulbulcus ibis</i>)	7	3	45	6.4	3	6					4	2	1	1
White Ibis (<i>Eudocimus albus</i>)	1		120		1									
Southern Lapwing (<i>Vanellus hilensis</i>)	2		40	20.0			2						2	
Bare-eyed Pigeon (<i>Columba corenisi</i>)														
Chestnut-fronted Macaw (<i>Ana severa</i>)	6		60	10.0	3	4							5	1
Yellow-headed Parrot (<i>Amazona ochrocephala</i>)	9		90	10.0	5	7							9	
Orange-winged Parrot (<i>Amazona amazonica</i>)	5	1	55	11.0	2	3							5	
Smooth-billed Ani (<i>Crotophaga ani</i>)	12	5	65	5.4	7	6							9	3
Lineated Woodpecker (<i>Dryocopus lineatus</i>)	3		40	13.3	2	1							3	
Tropical Mockingbird (<i>Mimus gilvus</i>)	2		10	5.0		2							2	
Oriole (<i>Icterus spp.</i>)	1		10		1								1	
Red-breasted Black Bird (<i>Leistes militaris</i>)	2		15	7.5	1	1							2	
N = 50		10	550		25	32								
% Total = 31.3		22.2	10.0		27.5	26								
Totals = 159		45	5485		91	123								

¹ R = Response, NR = No response
² S = Silent, K = Klee, C = Chitter

³ D = Direct chase, P = Pendulum attack, R = Retreat,
C = Circle, W = Watch

Table 5. Predation and provisioning by American Kestrels at El Bayuelo, Venezuela.

PREY	♂					♀				
	BIOMASS		TRANS-FER			BIOMASS		TRANS-FER		
	N	% CAPTURE	WT. (G)	%	PREY	N	N	% CAPTURE (N = 129)	WT. (G)	%
Insect ¹	269	78.9	188.3	31.3	63	114	88.3	79.8	44.1	47.0
Lizard ²	69	20.2	414.0	68.7	58	15	11.6	90.0	34.8	53.0
Snake	1	0.8			1					
Mouse	1	0.8			1					
Bird	1	0.8			1					
Unknown ³	29				11	7				
Cache ³	11					2				
Failed	<u>146</u>					<u>49</u>				
	527					187				
PREDATION										
		♂				♀				
		\bar{x}	S.D.	N	\bar{x}	S.D.	N			P
Perch Height (m)		8.1	5.0	269	7.2	3.3	72			NS
Distance to Prey (m)		25.0	19.7	407	25.3	16.2	149			NS
Time on Ground (sec)		7.9	10.4	246	5.9	6.7	85			NS
Perch Height & Insect Capt. (m)		8.6	5.8	157	7.2	3.2	60			NS
Perch Height & Lizard Capt. (m)		8.6	4.8	28	9.8	1.4	7			NS

¹ Mean weight of insect = 0.7 g.² Lizard (3 spp.) = 6.0 g.³ Not included in calculation.

of 53.0 before provisioning (Table 5). Production feeding allowed females to consume a preponderance of lizards, representing 89% by biomass. Males therefore, increased the female's diet of lizards by some 36%. From 2 closely observed pairs which did not produce eggs, none to few lizards were captured or transferred to the females. Both adult females were frequently seen "begging" for food and hunting for themselves. Upon examination, these females exhibited none to slight ovarian development. Apparently these individuals were not receiving sufficient amounts of food for egg production.

Nest Sites. Palm, Ceiba (*Ceiba pentandra*) and Araguaney (*Tabebuia chrysantha*) provided nest sites for breeding pairs. Excavations by woodpeckers (*Melanerpes* spp., *Dryocopus* spp., *Campephilus* spp.) provided protected cavities. Mean height of 22 nests was 7.8 m. Palms held 12 of 22 nests under study. Nest entrances favored a N-S aspect which faces into prevailing winds from the north and south.

Pairs 1A and 2A lost their nests to wind and fire,

respectively. Both pairs renested in the same kind of trees and new nests also faced into the wind: entrance changed from SW to SE and from SW to N, respectively. Topography, botanical features, and perhaps adjacent conspecific pairs were factors in nest site location (see also Bowman and Bird 1986). Pair 3C nested in a palm which also contained nests of Yellow-headed Parrots (*Amazona orchocephala*) and Tropical Screech Owls (*Otus asio choliba*).

Eggs and Young. Because of the difficulty of climbing nest trees, especially palms, relatively few data were recorded for kestrel eggs and young. One clutch of 4 eggs (\bar{x} Width = 27.8 mm, \bar{x} Length = 35.8 mm), pair 4A, lost an average of 5.2% of the total weight (58–55 g) from day 13–20 of incubation.

Counts of fledged young from 9 nests suggest a production of 2–3 young/pair. Pair 3C produced 3 eggs, hatched 1 male and 2 females but fledged only 1 of each sex. From direct counts on collected females, 12 females possessed 44 *corpora lutei*, suggesting 3.7 (range 2–5) probable eggs/females. From

5 nests in El Bayuelo, the date of first egg laid ranged from 17 January–14 February (29 d).

Predation. Insects and lizards comprised the majority of the prey (Table 5). Kestrels hunted almost solely from perches. Only incidental occurrences of hawking or hovering flights were recorded. Hunting was reduced during the "hot" or mid-day period from 1200–1500, unlike kestrels in California which maintained an even rate of daily hunting activity (Balgooyen 1976). Both populations captured prey with similar success (California = 70%; Venezuela = 73%). During periods of high temps (36°C), kestrels in Venezuela perched in the shade, gasped and panted, and held contour feathers tightly to the body. Wings were kept open.

From 100 consecutively timed prey deliveries to the nest, kestrels in California captured prey items an average of 5.1 min each (S.D. = 5.6 min). In a similar test of 159 prey items, kestrels in Venezuela secured prey every 10.8 min (S.D. = 13.1), the difference being highly significant ($t = 4.14$; $P = 0.001$). On a daily basis this translates to 175 prey items/15 hr in California being provided by the adults compared to a maximum of some 70 prey items/12 hr being brought to the nest in Venezuela.

Kestrels perched an average of 7.7 m above the ground ($N = 341$). Distance from falcon to prey averaged 25.2 m ($N = 556$). For either sexes perch height and strike distance were not correlated ($r = 0.22$, $N = 345$). Mean successful capture distance was significantly shorter ($P = 0.001$) than the mean failure distance (28.7 m; S.D. = 20.3, $N = 266$ vs. 23.0 m, S.D. = 16.2, $N = 379$). Comparison of the mean capture distance of falcon to lizard (34.2 m, S.D. = 20.7, $N = 48$) versus that of insects (21.6 m, S.D. = 16.4, $N = 329$) indicates that insects were expectedly more difficult to obtain or detect than lizards as strike distances increase ($t = 3.3$; $P = 0.001$). Kestrels (either sex) did not however, change their perch height when hunting lizards or insects (lizards $\bar{x} = 8.7$ m, S.D. = 4.8, $N = 35$; insects $\bar{x} = 8.2$ m, S.D. = 5.7, $N = 217$) (Table 5).

Of 714 observed strikes by kestrels, males accounted for 527 attacks. Differences in sexual roles during breeding biases hunting frequency in favor of males. Captures were successful on 72.7% of all attempts, and there was no significant differences between the sexes in capture success.

Caching. All pairs and both sexes practiced caching. Cached items were exclusive to the individual making the deposit. While most individuals utilized

fewer sites, the male of pair 1 utilized up to 11 cache sites. Unlike kestrels in California, most caches in Venezuela were located on the ground (58%, $N = 24$), contained anolid and iguanid lizards (96.4% $N = 28$ caches) and were emptied by afternoon. Other caching sites included fence posts, telephone poles, dead branches, and epiphytes.

Dust Bathing. In the evening (time range 1716–1901 H, $N = 6$ females, 2 males) kestrels sought dirt roadways to dust bath. Typically, an individual lands on a roadway and walks to a spot where cattle or vehicles have loosened the surface. While crouched on bent tarsi and with the head lowered, an individual scratches and flaps to bring up dust. The tail is held open. Rotation or side to side rocking of the body was commonly observed. Air temperatures ranged from 32–34°C; one substrate recording reached 37.2°C. After dusting, females commonly flew to the nest cavity.

DISCUSSION

Despite differences in botanical composition between breeding territories in North and South America, kestrels inhabit physiographically comparable landscapes. Grassland (pasture)-forest ecotone provides kestrels with nesting cavities, open flatland vegetation in which to hunt, numerous perches and suitable prey. In addition to habitation events in the kestrel's natural history appeared to follow a similar pattern in both areas. Noteworthy in comparison included the establishment of a defended territory, pair bonding, production feeding, female centripy, selection of a nest site, vocalizations, hunting, care and defense of young and caching. Apparent differences were quantitative and included kestrels from Tachira inhabiting relatively small territories, hunting and provisioning at lower rate, capturing fewer mammals and birds, defending more against inter-specific food competitors, and generally producing fewer young than kestrels in California.

While avoiding midday periods, kestrels in Venezuela preyed on insects and small lizards in comparatively small territories (Table 3), suggesting a high prey density (Lack 1954; Craighead and Craighead 1956; Stenger 1958; Gill and Wolf 1975; Newton 1976, 1979; Meyers et al. 1979; Village 1982; Bowman and Bird 1986). While predation success is similar in both areas, rate of feeding young by Venezuelan adults is relatively low when compared to rates in California (for invertebrates 5 min vs. 11 min). Apparently, low prey density, few young being

produced at El Bayuelo or perhaps both factors account for a low feeding rate.

Kestrels of El Bayuelo capture small lizards and invertebrates, but rarely take mammals or birds. Personal observation of all territories suspects unavailability. At El Bayuelo a random sample of 65 snap trap-nights over the course of the study resulted in no small mammals captured. Likewise, small birds were very rarely seen in kestrel territories. Both Jenkins (1969) in Costa Rica and Cruz (1976) in Jamaica reported none to few mammals and birds in kestrel territories, and, consequently, insects and lizards constituted the majority of the diet. Kestrels in North America are predators of abundant small and/or large prey during the breeding season (Heintzelman 1964; Smith et al. 1972; Sparrowe 1972; Collopy 1973; Balgooyen 1976; Craig and Trost 1979; Bohall-Wood and Collopy 1987). In Venezuela however, by being predators of small prey, kestrels may not obtain sufficient energy to produce relatively large clutches or, at times, even forego reproduction. One observation from a clutch of 2, showed 1 sibling (103 g) uncommonly below the mean adult female weight of 108 g and the weight of her female sibling (124 g).

Harvesting small prey may not only influence levels of production, but size of territory as well. Kestrel territories from El Bayuelo are only 5.2% the mean size of territories recorded elsewhere (Table 3). Small prey are energy "expensive" and do not allow efficient capture, transport and preparation by kestrels (Newton 1979; Orians and Pearson 1979). Energy expended over distance traveled becomes increasingly prohibitive as payload energy diminishes; thus, relatively small territories and low production. At El Bayuelo, several pairs did not or could not breed. An examination of ovaries suggests insufficient energy intake.

Compared with kestrels in California, Venezuelan pairs frequently drive several insect and lizard-foraging competitors from their territories (Table 4). Cattle Egrets (*Bubulcus ibis*), Southern Lapwings (*Vanellus chilensis*), Smooth-billed Anis (*Crotophaga ani*), Yellow-headed (*Milvago chimachima*) and Crested Caracaras (*Polyborus planus*), Roadside Hawks (*Buteo magnirostris*), Black-shouldered Kites (*Elanus caeruleus*), Savanna Hawks (*Heterospizas meridionalis*), and others were excluded from breeding territories, suggesting a need not to defend young but to protect a prey base. A small territory would facilitate defense. An ecological equation involving

frequent territorial defense and capturing small expensive prey is balanced by kestrels inhabiting comparatively small territories and producing few young.

Kestrels in California rarely, if ever, transferred insects. In Venezuela, 23% (63 of 269) of the insects captured were transferred by males. Differences between the 2 populations may reflect unavailability of mammals and birds on kestrel territories in Venezuela as well as the need to provide food to females

In a study conducted near Davis, California, Rudolph (1982) observed 1 kestrel pair expending more energy during production than other pairs. The female regularly hunted, both sexes hunted close to the nest cavity, and both took small invertebrate prey. Rudolph felt that low vertebrate availability was the cause but did not provide the size of the pair's territory. Since only 2 young were produced there could be a limit to energy gained by this strategy in relatively poor territories (see Newton 1976). Except for regular female hunting, a similar pattern was observed in Venezuela.

Kestrels in Venezuela display a breeding biology similar to pairs from North America. Production feeding, female centripy and general role behaviors of the sexes typify kestrels of both Americas. Similarity in natural history of breeding kestrels from North and South America does not reject hypotheses of size, sexual dimorphism (SSD) which are based on laws of energy (see Reynolds 1972; Balgooyen 1972, 1976; Mosher and Matray 1974; c.f. Mueller 1986).

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OBSERVATIONS ON POST-FLEDGING DEPENDENCE OF KESTRELS (*Falco tinnunculus rupicolus*) IN AN URBAN ENVIRONMENT

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ABSTRACT.—Observations were made of duration of post-fledging dependence period (PFDP), behaviour, body mass and food requirements of artificially released Kestrels (*Falco tinnunculus rupicolus*) in urban Windhoek, Namibia. Mean PFDP was 41.5 d, slightly longer than recorded for Kestrels in temperate areas. Daily gross energy intake of captive fledglings was 256 kJ/d; similar to fledglings in temperate areas.

The southern African race of the Kestrel (*Falco tinnunculus rupicolus*) is widespread, common and has adapted to urban existence. The species is almost completely unstudied in southern Africa (Steyn 1982), which contrasts with temperate populations of the nominate race (*F. t. tinnunculus*) where detailed studies have been made of diet and energetics (Kirkwood 1979; Village 1982a; Masman et al. 1986), territoriality (Village 1982b; Pettifor 1983), breeding (Cavé 1968), moult, ageing and sexing (Village et al. 1980), and movements, mortality and distribution (Newton 1979; Cramp and Simmons 1980; Cade 1982).

At least 4 breeding sites occur within the inner city limits of Windhoek, Namibia, an area of about 12 km². The same nesting sites and home ranges have been used in consecutive years, unless disturbed by humans (JK, unpubl. data).

In temperate areas Kestrels have a diet consisting almost entirely of small mammals, especially the Common Vole (*Microtus arvalis*) (Masman 1983). There is evidence of differences in body size, productivity, lifespan and diet between the temperate and tropical populations of the species (Steyn 1982; Tarboton and Allan 1984; Kemp 1985; A. S. Robertson, *in litt.*; see also Cavé 1968; Newton 1979; Cramp and Simmons 1980).

Fledgling period is a time of high mortality for most avian species and may be one of the most critical periods of the avian life cycle (Newton 1979, 1984). First-year mortality has been reported to account for more than half of all recorded mortalities in European Kestrels (Cavé 1968; Newton 1984). Our study describes aspects of post-fledging dependence period (PFDP) of Kestrels in urban Windhoek, Namibia in 1984 and 1987.

METHODS

In February 1984 five unsexed, prematurely fledged kestrels were obtained from a human-disturbed nest site in Windhoek, Namibia (22°33'S, 17°10'E). The birds were maintained in captivity until 10 d after their estimated fledging age (30–34 d of age; JK, unpubl. data; Steyn 1982; Maclean 1985), and then released. Over the same period another urban nest containing 3 nestlings was monitored until the last fledgling disappeared from the vicinity of the nest site.

During 23–27 October 1987 four unsexed, prematurely fledged kestrels were captured below a Windhoek city building. One bird was unable to fly, had a low body mass and was particularly timid. The remaining 3 birds flew clumsily, but were readily caught. Two adult kestrels were in attendance during this period, and circled overhead or perched nearby when the young birds were captured. Judging from their inability to fly properly and incomplete growth of tail and wing feathers, these kestrels were near fledging age (30–34 d of age). On 2 November the birds were colour-ringed and weighed. On 4 November the fledgling kestrels were released.

Five fledglings held in captivity in 1984 were fed a diet of day-old-chicks, raw lean beef and a dietary supplement (Beefee, Centaur Product). The 1987 kestrels were fed a diet of raw lean beef, white mice, mealworms, locusts and crickets, as well as a dietary supplement. Water was available at all times. Food was provided twice daily for the first 10 d after release. Thereafter, food was provided once daily until about 10 d after the last bird was seen at the release-site.

Daily "wet" food intake was measured gravimetrically for the 5 fledglings in 1984 during an outdoor feeding trial which lasted 7 d. Wasted food and pellets were accounted for with corrections for dessication. Fledglings were weighed before and after the feeding trial, and inclement weather, ambient temperature and behavioural activities were noted daily during the trial. Mean daily food intake was determined by dividing the group's gross daily food intake by the number of birds in the group. Daily gross energy intake of fledglings was calculated from weight of food provided less wasted food and pellets, and known energy values of the food (Komen 1986).

Table 1. The PFDP of Kestrel fledglings released from captivity in 1987, compared with longest PFDP recorded for captive fledglings released in 1984, and that of wild fledglings observed in 1984. Column D represents the number of days between release date and first foraging absence of longer than 48 hrs. Data for White ring bird [in square brackets] represents combinative PFDP at primary and surrogate feeding site.

KESTREL IDENTITY	PFDP DAYS	A		B/A		C		COLUMN D DAYS	
		NO. OF DAYS FLEDGLINGS RETURNED TO RELEASE SITE		NO. OF DAYS FLEDGLINGS NOT SEEN AT RELEASE SITE		C/A			
		%	%	%	%	%	%		
1987									
Black ring	47	38	81	9	19	—	—	34	
Yellow ring	54	36	67	18	33	—	—	21	
Orange ring	42	28	67	14	33	—	—	17	
White ring	26	23	89	3	11	—	—	26	
[White ring]	82	57	70	25	30	—	—	26]	
1984									
Captive fledglings	43	—	—	—	—	—	—	—	
Wild fledglings	37	—	—	—	—	—	—	—	
Mean*	41.5	36.4	74.8	13.8	25.2	—	—	24.8	
±S.E.	3.9	5.8	4.4	3.8	4.4	—	—	2.9	

* Excludes combinative PFDP of White ring bird in square brackets.

PFDP = Post-fledging dependence period.

Duration of post-fledging dependence period (PFDP) was calculated as the number of days from release to last return to the release site.

RESULTS

Duration of Post-Fledging Dependence Period. All 1987 fledglings were seen daily until 19 November, 26 d after release. Individual birds were then seen occasionally until 28 December (54 d after release), the last time any bird was seen at the release site.

The first bird to disappear, 26 d after release (White ring; Table 1), was reported 7 d later at a homestead about 40 km north of Windhoek. The bird was feeding largely independently, but occasionally took meat put out in the evenings and was reported to be quite tame (A. Mittendorf, pers. comm.). The bird was seen occasionally until 25 January, 50 d after adopting the surrogate feeding site.

The longest PFDP recorded at the primary release site was 54 d (Yellow ring). The Yellow ring fledgling was in poor condition at time of capture. In 1984 the last day on which a wild fledgling was seen near the nest-site was 37 d after fledging. In 1984 the last captive fledgling to be seen at the release site was 43 d after date of release (Table 1). Mean

PFDP for all fledglings, excluding the White ring fledgling's extended PFDP, was 41.5 d (S.E. = ± 3.9 d).

As a measure of feeding independence, the shortest period recorded from release to first foraging sortie lasting a minimum of 2 d was 17 d (Orange ring). The longest period was 34 d (Black ring). A measure of feeding dependence, the number of days on which fledglings returned to feed at the release site during PFDP, ranged between 67% and 89% of total PFDP (Table 1).

At least 3 of 9 artificially released fledglings survived after their PFDP, and 1 reached adulthood. One 1984 fledgling was recaptured and released about 6 km from the release site, 105 d after initial release. Another 1984 fledgling was resighted carrying food about 1 km from the release site 485 d after date of release. A 1987 fledgling (Orange ring) was resighted perch-hunting about 4 km from the release site, 224 d after release.

Behaviour of Fledglings. During the first week after release, fledglings were noticeably clumsy in flight and landing technique. Fledglings spent much of their time exercising with wing flapping from rooftops, trees and telephone poles. Most activities were accompanied by frequent and noisy calling. Fledglings occupied the day with exercise, play, and

Table 2. Body mass (grams) of unsexed pre-fledging and post-fledging Kestrels, indicating change in body mass, number of days between first and last dates of weighing (Column D), and daily change in body mass (grams/day). Data for 1984 captive fledglings also represent body masses pre- and post-feeding trial (see Table 3).

BIRD IDENTITY	PRE-FLEDGING BODY MASS (GRAMS)	POST-FLEDGING BODY MASS (GRAMS)	CHANGE IN BODY MASS (GRAMS)	COLUMN D (DAYS)	DAILY CHANGE IN BODY MASS (GRAMS/DAY)
1987					
Black ring	190	220	30	6	+5.0
Yellow ring	165	210	45	10	+4.5
Orange ring	185	210	25	6	+4.2
White ring	180	215	35	6	+5.8
Mean	180.0	213.8	33.8		
±S.E.	5.4	2.4	4.3		
1984					
Captive fledglings					
31285	190	203	13	8	+1.6
31302	185	173	12	8	-1.5
31287	205	173	32	8	-4.0
31286	205	193	12	8	-1.5
31288	185	173	12	8	-1.5
Mean	194.0	183.0	16.2		
±S.E.	4.6	6.3	4.0		
Wild fledglings					
31284	200	—			
31283	190	—			
31301	210	—			
Mean	200.0				
±S.E.	5.8				

preening but remained within a radius of about 50 m of the aviary most of the time. Mock stalking and "capture" of objects representing prey (e.g., stones, grass tufts, etc.) were recorded on a number of occasions, mostly on the ground. Fledglings remained close together most of the time, bathing together, and allopreening was noted on a few occasions. Curiosity movements, including frequent head inversion (*sensu* Sherrod 1983) were particularly noticeable during the first week after release. Fledglings huddled together on the feeding platform at night.

During the second week after release individuals ranged further from the aviary, and 2 fledglings were seen catching lizards and insects on the ground. Fledglings attempted to steal food items from one another, even when excess food was available. Individuals asserted themselves, mantling food and calling loudly when siblings came too close. Aerial manoeuvrability and judgement for landing space

and prey items improved noticeably by the end of the third week after release. By this stage fledglings roosted alone among foliage of tall trees near the aviary.

Wild fledglings observed in 1984 performed simple aerial movements, and group play on ledges near the nest-site, including stalking and "capture" of prey remains. At later stages we observed a few aerial chases by fledglings of parent birds and siblings, and of other bird species [1 incident of a playful and loudly vocal "attack" on a Black Kite (*Milvus migrans*) and 2 incidents of chasing Palewinged Starlings (*Onychognathus nabouroup*)]. Adult-fledgling food transfers were initially conspicuous by the submissiveness of fledglings, but fledglings became progressively more aggressive during food provision. Food transfers were initially associated with subdued fledgling vocalization, but calling later became more intense.

Table 3. "Wet" food intake (day-old-chicks (DOC) and raw lean beef (meat)) and daily gross energy intake (E) of five fledgling Kestrels during an outdoor feeding trial in 1984. Daily inclement weather, minimum and maximum ambient temperature and notes on activity are recorded.

DATE DD/MM	DOC/ BIRD GRAMS	E KJ WET*	MEAT/ BIRD GRAMS	E KJ WET*	SUM OF E kJ/ BIRD/ DAY	WEATHER	T _A (°C)		ADDITIONAL NOTES
							MIN.	MAX	
24/2	0.0	0.0	50.0	296.5	296.5	slight breeze, partially cloudy	17	31	very active, frequent flying, play
25/2	56.0	301.8	0.0	0.0	301.8	light breeze, partially overcast, late afternoon drizzle	19	33	active, some flying and play
26/2	34.6	186.5	0.0	0.0	186.5	no wind, overcast, late afternoon drizzle	20	31	active, some play
27/2	35.0	188.7	4.4	26.1	214.8	light breeze, overcast, late afternoon rain	19	30	active, some play
28/2	7.0	37.7	21.2	125.7	163.4	no wind, partial overcast	19	31	inactive most of day
29/2	14.0	75.5	32.4	192.1	267.6	light breeze, partially cloudy, afternoon rain	20	31	active, some flying, play
01/3	32.0	172.5	32.0	189.8	362.3	light breeze, partially overcast, no rain	17	30	very active, frequent flying and play
\bar{x}					256.1		19	31	
±S.E.					26.9		0.5	0.4	

* Energy content of food consumed; DOC = 5.39 kJ/g "wet," meat = 5.93 kJ/g "wet"; "wet" represents "wet" or fresh weight of food (Komen 1986).

The first prey-items believed to have been captured by individual wild fledglings included 2 large locusts (about 2 wks after fledging), and, at a later stage, a Striped Mouse (*Rhabdomys pumilio*). The adult birds were providing primarily *Agama* spp. lizards (e.g., *Agama planiceps*) to the fledglings, although other lizards (*Cordylus*, *Cordylosaurus* and *Pedioplanis* spp.), locusts, crickets and a few small birds were also recorded.

Body Mass and Food Intake of Fledglings. Table 2 presents body mass data for 3 wild pre-fledgling birds, 5 fledglings held in captivity in 1984 and 4 held in captivity in 1987. Mean pre-fledgling body mass for all birds was 190.8 g (S.E. = ± 3.6 g; N = 12) and mean post-fledgling body mass was 196.7 g (S.E. = ± 6.4 g; N = 9). There was no significant difference between pre- and post-fledgling body mass (Student's *t*-Test; *t* = 0.8401; df = 19; *P* = 0.4113). However, the 1987 fledglings showed a gain in body

mass ($\bar{x} = 33.8$ g \pm S.E. = 4.3 g, N = 4; or 4.9 g/d) between pre-fledgling and post-fledgling weighing dates, whereas during the feeding trial in 1984, 4 of 5 fledglings showed a loss in body mass over a period of 8 days ($\bar{x} = 16.2$ g \pm S.E. = 4.0 g, N = 4; or 2.1 g/d).

Table 3 presents a breakdown of fledgling daily "wet" food intake and daily gross energy intake daily gross energy intake was calculated as 256.1 kJ/d (S.E. = ± 26.9 kJ/d).

DISCUSSION

Disparity exists in the amount of information available for tropical versus temperate populations of the Kestrel. In southern Africa Steyn (1982) reported that Kestrel PFDP lasted about 1 mo, following a nestling period of 34 d. In the present study, mean duration of PFDP was 41.5 d; PFDP of the European Kestrel has been reported as being between

3.5–4 wks (Newton 1979) and 30 d (Masman 1983). Such implies that tropical, urban fledglings require about 11 d longer to become independent. During a comparative study of artificial and wild Peregrine Falcon (*Falco peregrinus*) fledglings, Sherrod (1983) showed that PFDP of wild fledglings appeared to be longer. Smaller male Peregrine Falcons had shorter PFDPs than female fledglings, and Sherrod cautioned that environmental constraints such as food resource might affect the duration of PFDP from season to season.

Excess food available to artificially released Kestrel fledglings did not apparently delay independence or ultimate dispersal [all dispersed when food was still supplied; see also Sherrod (1983)]. When released artificially, young kestrels are well fed and do not have to compete among themselves for food and are free to wander and experiment with flying and hunting. At some stage they learn to hunt for themselves, and then spend more time and energy finding and killing their own prey.

Daily gross energy intake of captive fledglings in this study was 256 kJ/d and probably as high as would be expected for wild fledglings at high daily ambient temp (Table 3; cf. Masman 1983; Masman et al. 1986). Indirect support rests with the fact that 4 of 5 fledglings lost weight during feeding trials. Kirkwood (1980) showed the gross energy intake of young free-flying, temperate Kestrels to be 251–276 kJ/d; similar to Kestrels in this study. The highest mean daily gross energy intake recorded for active adult Kestrels feeding young in temperate areas has been reported as 594 kJ/d (Masman et al. 1986).

Gross energy values of lizards vary according to species, size, condition and season, but are probably close to 5.7–6.3 kJ/g “wet” (C. S. Sapsford, pers. comm.). Accordingly, a daily gross energy intake of 256 kJ would require the consumption of between 41–45 g of lizards. In the Windhoek area equivalent intake would be 2–3 medium sized *Agama planiceps* lizards (mass range 4–38 g; JK, unpublished data).

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RESPONSES OF BREEDING AMERICAN KESTRELS TO LIVE AND MOUNTED GREAT HORNED OWLS

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ABSTRACT.—Behavioral responses of American Kestrels (*Falco sparverius*) to a live and taxidermic mount of a Great Horned Owl (*Bubo virginianus*) were studied during 2 breeding seasons in southwestern Quebec. Kestrels responded less aggressively to taxidermic mounts, particularly as distance of the owl from the nestbox increased. Intensity of aggression did not increase from incubation to nestling period. Aggressive response to live owls suggests that Great Horned Owls are recognized as potential predators of fledgling kestrels.

Interspecific aggression by raptors during the breeding season is poorly documented. Most raptors defend territories against conspecifics, but raptors occasionally exhibit aggressive behavior toward ecologically similar species as a result of competition for food and breeding territories (Mikkola 1976; Bluhm and Ward 1979). Predation on other raptor species is uncommon, although Great Horned Owls (*Bubo virginianus*) are known to kill raptors as large as Northern Goshawks (*Accipiter gentilis*) (Newton 1979). Kerlinger and Lehrer (1982) reported that migrating Sharp-shinned Hawks (*A. striatus*) recognized a Great Horned Owl model, aggressively attacking from distances > 30 m, suggesting that Sharp-shinned Hawks may frequently be preyed upon by Great Horned Owls and hence display aggressive behavior toward the owl in daylight hours.

During nest establishment, American Kestrels (*Falco sparverius*) direct aggressive behavior primarily against non-raptorial cavity nesters, perhaps due to competition for nest sites. Kestrel aggression toward other raptors increases throughout the breeding season and peaks as the young fledge (Balgooyen 1976).

Our study tests whether aggressive behavior by American Kestrels toward Great Horned Owls varies with respect to stage of the reproductive period and distance from the nest. As Knight and Temple (1986a) pointed out, many studies of avian nest defense assume, without testing, that parents behave similarly to taxidermic mounts of potential predators as to a living bird. We examined whether kestrels react similarly to a live bird and a mounted specimen.

STUDY AREA AND METHODS

Our study was conducted on the western end of the island of Montreal, Ile Perrot and eastern sections of Vau-

dreuil-Soulanges County in southwestern Quebec. Tests were performed on kestrels breeding in nestboxes erected by the Macdonald Raptor Research Centre, primarily in northern hardwoods in hedgerows bordering fallow agricultural fields. Data were collected on 9 nests from mid-incubation to mid-nestling stage from 16 May–14 July 1982. Six nests were tested during the mid-nestling stage from 20 June–6 July 1985.

We presented a live and a taxidermic mount of a Great Horned Owl to all nests to examine parental behavior. Each live owl was tethered to a perch with leather jesses but was allowed unrestricted body movement. Each mounted owl was placed on a post in an upright position with ear tufts raised and wings folded against the body. Each mounted owl was positioned so as to face directly toward a nestbox. To increase conspicuousness to the kestrels, both versions of the owl were raised above the level of the surrounding vegetation. In 1982 each version was tested at 10, 50, and 100 m distance from the nest. Each stimulus was tested from farthest to nearest distance in consecutive tests within a single day. Sequence of presentation of live and mounted versions was randomly chosen at all nests. To avoid excessive disturbance at least 1 d elapsed between trials with a live and mounted owl. In 1985 both stimuli were tested at 10 and 100 m, as was a live, white, Leghorn Chicken (*Gallus domesticus*) used as a control. The chicken was dyed with brown shoe dye to mimic owl coloration. In 1985 6 tests/nest (3 stimuli at 2 distances) were performed randomly at 2 d intervals to lessen habituation by the kestrels. After placement of each bird, observers retreated to a position approximately 100 m from the nestbox before recording observations. Within each year all observations were performed by the same observers to eliminate potential bias caused by novel intruders.

Two categories of aggressive behavior, number of dives and “klee” vocalizations, were recorded over a 10-min period. Each “klee” in an uninterrupted series of calls was counted as a separate vocalization. Dives resembled the pendulum attack as described by Balgooyen (1976). Aggressive behavior by both parents was summed to obtain total number of dives and vocalizations per test.

Data were analyzed using the Wilcoxon Signed Ranks test (Daniel 1978), and $P < 0.05$ was used for determining statistical significance.

Table 1. Intensity of aggressive responses of breeding American Kestrels to live and mounted Great Horned Owls during mid-incubation and mid-nestling stages 1982 and mid-nestling stage 1985.

STIMULUS AND DISTANCE	NO. OF PAIRS REACTING	CALLS/10 MINS*	DIVES/10 MINS*
		($\bar{x} \pm 1$ S.D.)	($\bar{x} \pm 1$ S.D.)
a) Mid-incubation 1982			
Owl 10 m	6/9	9.67 \pm 10.31 ^a	5.56 \pm 6.11 ^a
Owl 50 m	7/9	7.11 \pm 9.67 ^{abc}	3.89 \pm 8.39 ^a
Owl 100 m	4/9	4.33 \pm 6.69 ^{bc}	3.78 \pm 6.61 ^{ab}
Mount 10 m	5/9	14.56 \pm 8.84 ^{ab}	4.56 \pm 5.34 ^{ab}
Mount 50 m	2/9	3.44 \pm 8.05 ^c	2.11 \pm 5.97 ^b
Mount 100 m	2/9	6.67 \pm 13.31 ^{abc}	5.22 \pm 13.89 ^{ab}
b) Mid-nestling 1982			
Owl 10 m	8/9	17.11 \pm 26.07 ^a	6.44 \pm 9.10 ^{ab}
Owl 50 m	7/9	11.33 \pm 21.00 ^a	5.00 \pm 10.25 ^{ab}
Owl 100 m	6/9	13.11 \pm 19.64 ^a	4.89 \pm 10.67 ^b
Mount 10 m	5/9	11.55 \pm 14.63 ^a	8.56 \pm 13.35 ^a
Mount 50 m	1/9	0.11 \pm 0.33 ^b	0 ^c
Mount 100 m	2/9	0.33 \pm 0.70 ^b	0.22 \pm 0.67 ^c
c) Mid-nestling 1985			
Owl 10 m	6/6	84.00 \pm 52.46 ^a	28.33 \pm 19.72 ^a
Owl 100 m	3/6	33.17 \pm 57.09 ^b	11.83 \pm 20.77 ^a
Mount 10 m	2/6	5.67 \pm 11.20 ^{bc}	0 ^b
Mount 100 m	0/6	0 ^c	0 ^b
Chicken 10 m	0/6	0 ^c	0 ^b
Chicken 100 m	1/6	0.83 \pm 2.04 ^c	0.17 \pm 0.41 ^b

* Values within a column that share a common superscript are not significantly different ($P > 0.05$).

RESULTS

During mid-incubation in 1982, a mounted owl at 50 m provoked the lowest mean number of dives and klees (Table 1a). During mid-nestling stage, a mounted owl at 50 and 100 m elicited significantly fewer vocalizations and dives from parents than all other stimuli (Table 1b). There were no significant differences in responses elicited by a live owl at all 3 distances and the taxidermic mount at 10 m, except that significantly fewer dives were directed at the owl at 100 m when compared to the mount at 10 m.

There was no significant increase in the number of dives or vocalizations performed by parents from incubation to nestling stages for the live owl at all distances or the mounted owl at 10 m.

In tests performed during mid-nestling stage in 1985 a live owl elicited significantly more vocalizations and dives at both distances than the other 2 stimuli (Table 1c). Significantly more vocalizations were directed at the live owl at 10 m than at 100 m, but there was no statistical difference with respect to number of dives. All pairs of kestrels reacted to

the presence of the live owl, but not the taxidermic owl mount or chicken. Only 2 pairs of birds reacted to the taxidermic mount at 10 m and 1 pair responded with a low level of aggression to the chicken at 100 m.

Both sexes participated in aggressive displays. In 8 of 12 trials in 1985 where kestrels behaved aggressively toward any of the 3 stimuli, both birds were involved. In the remaining 4 cases, only the female was observed displaying aggressive behavior. Males forage away from the nest while females remain near the nest (Balgooyen 1976), which probably accounts for differences in participation in aggressive acts between sexes. In trials where both parents were present, both emitted calls and dove at the stimulus.

DISCUSSION

In 1982 although the mean number of dives or vocalizations generally increased in all cases from incubation to nestling stages, nest defense behavior of individual pairs was highly variable. This factor

explains the lack of significant increases for dives or vocalizations performed by parents from incubation to nestling periods.

For altricial birds a model of optimal levels of parental defense predicts that the intensity of defense will increase with nestling age due to a decline in relative difference of expected future survival between parent and offspring (Andersson et al. 1980). Since the American Kestrel is a cavity nester, eggs and nestlings are not easily accessible to Great Horned Owls. Parents might be expected to exhibit a low level of nest defense throughout the egg and nestling stages to discourage Great Horned Owls from remaining in the vicinity of the nest. Intensity of aggression should not increase as long as nestlings remain in the nest and risk of predation is low. Furthermore, pendulum attacks such as those we observed often involve prolonged periods of vigorous flying, an energetically demanding activity (Gessaman 1980). Albeit rare, aggressive displays also carry the risk of injury or death by the owl. Parental aggression might be expected to increase significantly during the first few days post-fledging while young fly poorly and are more vulnerable to predation, although not tested in our study.

Knight and Temple (1986b) have suggested that observed increases in nest-defense intensity during the nesting cycle may be attributable to experimental methods. Repeated exposure of breeding birds to potential predators without resultant harm to young results in positive reinforcement and a loss of fear of the predator (Knight and Temple 1986b). In our study the mean number of dives and vocalizations generally increased from incubation to nestling stage in 1982, but none of the increases was statistically significant. Responses of individual pairs of kestrels were highly variable. Some pairs showed increased aggression in the nestling stage while others showed decreased aggression relative to the incubation stage. Our results do not suggest that positive reinforcement or loss of fear of the Great Horned Owl was occurring.

Our results from 1982 and 1985 indicate that parents do not react similarly to live and mounted owls and support those obtained by Knight and Temple (1986a) (i.e., taxidermic mounts may not be an accurate method of assessing aggressive behavior by parents). In 1985 1 pair of kestrels reacted with limited aggression toward the chicken. However, aggression occurred soon after the chicken was placed in the field and may have been directed to-

ward the observers. Consequently, kestrels appear able to differentiate a chicken from an owl as not being a potential threat to their young.

Several factors may account for differences observed in reactions of parents to live and mounted owls. Lack of movement by a mounted owl, or some other subtle cue, may signal kestrels that little threat to their young was being posed. When a mounted owl is placed far from the nest, parents may limit aggressive behavior to minimize the possibility of drawing the potential predator closer to the nest. However, when placed close to a nestbox, recognition of the owl's shape and proximity to their young may be sufficient to provoke an aggressive response without additional cues associated with a live owl (e.g., movement). Alternatively, inhibition of aggressive behavior may have occurred since the mounted owl was positioned to face directly at the nest box. Knight and Temple (1986a) claimed a similar inhibition took place when a live American Crow (*Corvus brachyrhynchos*) stared directly at mobbing Red-winged Blackbirds (*Agelaius phoeniceus*).

Results of our study indicate that American Kestrels recognize Great Horned Owls as potential predators of fledglings, a behavior which is likely innate. Similar tests should be performed outside the breeding season to determine if non-breeding adults regard owls as potential predators and react aggressively.

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OBSERVATIONS OF A ZONE-TAILED HAWK FAMILY DURING THE POST FLEDGING PERIOD

F. HIRALDO, M. DELIBES AND R. R. ESTRELLA

ABSTRACT.—Behaviour of a Zone-tailed Hawk (*Buteo albonotatus*) family were recorded during the post-fledging period at Michilia Biosphere Reserve in Durango, Mexico, from mid-July to mid-August 1981. Number of daily flights did not increase with time, but average time span for each flight increased as nestlings grew older. Juveniles repeatedly performed movements that imitated hunting behaviour of adults. Time spent by adults near the nest decreased following fledging of young. Adults delivered 5.9 ± 2.8 ($\bar{x} \pm S.D.$) prey items/d ($N = 10$ d); nestlings daily consumed an estimated 296 ± 130 g ($\bar{x} \pm S.D.$) daily. Amounts varied during the observation period. Differences in behaviour of both adults suggested that the parental role of each sex was different. Apparent aggression of adults towards young may be related to the development of juvenile flight and/or to dispersal. The family may have remained together away from the nest area, as probably occurs with other congeneric species.

Biology of the Zone-tailed Hawk (*Buteo albonotatus*) is among the least known of North American raptors (Hubbard 1974; Zimmerman 1976). No information exists on behaviour of families during the post-fledging period (Brown and Amadon 1968; Porter and White 1975; Matteson and Riley 1981). This paper describes the behaviour of a family in oak-pine forest at Michilia Biosphere Reserve in Durango, Mexico.

STUDY AREA AND METHODS

The Michilia Reserve is located in a transitional zone (2250 m) from high mountains to plateaus in the Western Sierra Madre (23°27'N and 104°18'W). Average monthly temperature varies between 12°C and 28°C and annual rainfall between 50 cm and 70 cm, falling mostly in summer (Gallina 1981).

The nest was located on the crown of an oak (*Quercus* sp.) 17 m in height on the side of a small ravine. Observations were made from 200 m away with 10 × 40 binoculars and a 40 × 25 telescope. Field work began when the 2 young seemed fledged (17 July 1981) and continued until 19 August when the juveniles apparently left the nest area. During this period, 11 d were spent observing the hawks' behavior from dawn to nightfall (approx. 0700 H-2000 H). Adults were distinguished by plumage characteristics observed in flight (one adult had a secondary broken). Individual nestlings were recognized by their sizes when observed side by side at the beginning of activity each day and then followed individually the rest of the observation period. Moreover each had different patterns of white spots on the breast. Prey consumed by the young were observed directly. Eighteen prey items had been partly consumed by adults. Weights used in biomass conversion were: Cotton Rat (*Sigmodon* sp.) 90 g; lizards 20 g; *Colaptes* sp. 125 g; *Sicalia* sp. 20 g. If partial prey items were seen then we have simply adjusted the appropriate conversion factor accordingly to what the parents brought (i.e., $\frac{3}{4}$, $\frac{1}{2}$, $\frac{1}{4}$, etc., of the prey). Time spent by young eating prey and

weight of prey species captured by us assisted in compiling approximations.

RESULTS

Nestling Activity. Young of *Buteo albonotatus* gradually increased distance roamed from the nest (Table 1); flight time similarly increased (Fig. 1). Higher number of daily flights did not increase with time, rather the average time span each flight took increased as fledglings grew older (Spearman rank correlation coefficient $r_a = 0.911$; $P < 0.01$; $df = 8$; $r_b = 0.897$; $P < 0.01$; $df = 8$). There was also a positive relationship between age and proportion of daily flights in which more elaborate forms of flight maneuvers, such as gliding and circling, were employed ($r_a = 0.953$; $P < 0.01$; $df = 8$; $r_b = 0.887$; $P < 0.01$; $df = 8$).

On 23 occasions (82.1%) nestlings did not show aggressive responses to predators that were observed near the nest (e.g., Turkey Vulture (*Cathartes aura*), $N = 17$; Red-tailed Hawk (*Buteo jamaicensis*), $N = 1$; Cooper's Hawk (*Accipiter cooperi*), $N = 1$; Raven (*Corvus corax*), $N = 4$). On 5 occasions, nestling "B" attacked intruders (*Cathartes aura*, $N = 2$; *Buteo jamaicensis*, $N = 3$).

During observation periods, juveniles repeatedly performed movements that imitated, and often exaggerated, hunting behavior of adults. Some of these behaviors (e.g., picking up small objects, "hunting" thick branches, etc.) are quite common in many raptors (Ficken 1977). Other behaviors observed were 1) "capturing objects": a juvenile would hurl itself, flapping its wings or diving, towards the tip of a thin tree branch, a pine cone, or a twig on the ground,

Table 1. Percentage of total observation time spent by 2 juvenile Zone-tailed Hawks (A and B) at different distances from the nest during post-fledging dependence period.

OBS. PERIOD		DISTANCE				N (MIN)
		IN NEST	<200 M	200– 400 M	>400 M	
1st week	A	61.7	38.3	0.0	0.0	3600
	B	9.2	90.2	0.0	0.0	3600
2nd week	A	3.5	82.6	12.8	1.0	1299
	B	0.2	96.8	0.0	2.9	1440
3rd week	A	8.5	81.8	5.7	4.0	1320
	B	6.1	83.7	5.7	4.5	1320
4th week	A	0.0	47.6	14.3	38.1	1320
	B	0.0	44.7	11.4	43.9	1320

and seize the object with its talons. Several times the young bird broke up the twig or pine cone and bit the object while in flight. Object capture was first observed during the third week ($N = 12$) and more often in the fourth ($N = 57$); 2) "hunting from a perch" while perched a juvenile would repeatedly look at the ground, then launch from its perch and "capture" a twig on the ground only to drop the twig as soon as flight was resumed. Perch hunting was observed twice in the last week.

Adult-Young Interactions. Time spent by adults near the nest decreased dramatically following fledging of young. In the first week, adult "A" remained in the defended area near the nest most of the time (78.3%), while "B" was rarely present (4.12%). During subsequent weeks, time spent near the nest by both adults was limited (4.1%, 0.0% and 0.2% for "A," and 0.8%, 4.3% and 2.0% for "B"). Adult "A" seemed to defend the area most of the time and attacked possible predators (*C. aura*, $N = 12$; *B. albonotatus*, $N = 1$; *B. jamaicensis*, $N = 4$; and *C. corax*, $N = 13$) 83.3% of the 30 times both were present; "B" responded aggressively only 12.5% of 8 encounters with potential predators (*C. aura*, $N = 2$; *B. jamaicensis*, $N = 1$; *A. cooperi*, $N = 1$; and *C. corax*, $N = 4$). Difference between the two responses was statistically significant ($G = 11.4$; $P < 0.01$; $df = 1$; G test, Sokal and Rohlf 1979).

Parents delivered prey to young who tore food apart and fed by themselves. Adults brought mostly Cotton Rats ($N = 20$) lizards (*Sceloporus* spp; $N = 26$) and small to medium-sized birds (*Sicalia* sp; $N = 2$, *Colaptes* sp. $N = 6$ and 6 unidentified birds).

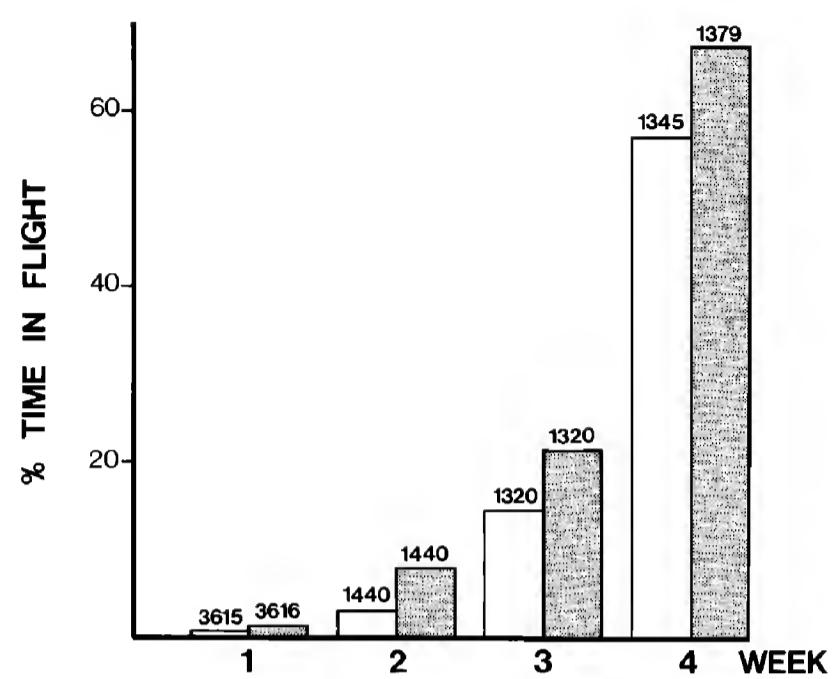


Figure 1. Percentage of total observation time spent in flight by juvenile from the first to the fourth observation week. Open bars: young A; Shade bars: young B.

Of 59 occasions during which the adults could be identified, "B" brought prey 40 times and "A" only 19, values different from those predicted by random sampling ($\chi^2 = 7.48$; $P < 0.01$; $df = 1$). Both adults usually carried food in their talons (96.8%; $N = 63$), although adult "A" carried small lizards in its beak on 2 occasions.

Nestlings begged for food with loud and continuous "chirps" as soon as one of the parents entered the nest area. Vocalizations were heard throughout the fledgling period and often occurred during the third and fourth weeks even when adults were not present. During the first week of observation, parents would most often bring food to where young were perched (93.3%; $N = 30$). In the later weeks the young would commonly approach adults for food (76.5% of observed food exchanges $N = 17$, in the second week; 90%; in the third week, $N = 30$ and 100% in the last week, $N = 6$). Prey was presented to the young in the nest during the first week (76.7%; $N = 30$) or on perches 100 m away. Later, feeding never took place in the nest. Feeding did occur 54.3% of the times within 100 m radius of the nest, 24.2% between 100 and 200 m, and 12.1% at >200 m between the second and fourth weeks of observation. Prey was transferred in the air only 9.3% ($N = 63$) of the time.

Adults delivered a mean of 5.9 ± 2.8 ($\bar{x} \pm S.D.$) prey items/d ($N = 10$ d) to the nestlings, which consumed an estimated 296 ± 130 g ($\bar{x} \pm S.D.$)

daily. Amounts varied during the observation period. During the first two weeks young received 352 ± 113.7 g ($\bar{x} \pm S.D.$) of food/d (N = 7), and during the last two weeks 165 ± 21.8 g/d (N = 3). In 18 out of 39 cases (46.1%) which we were able to see clearly, adults brought only portions of prey animals. Zone-tailed Hawks would not consume prey which fell on the ground (5%; N = 63). Of the remaining prey, 93% was consumed by a single nestling and 7% was consumed by both young at the same time.

Juveniles being harassed by adults or each other was often observed. One juvenile harassing the other occurred once in the second week, none in the third week and 10 times in the fourth. Adults were observed to harass their young 8 times during the final week of observation.

DISCUSSION

Young of *Buteo albonotatus*, like those of other raptors, gradually increase the distance roamed from the nest and progressively develop flight techniques (Johnson 1973; Harper 1976; Kussman 1977; Sherrod 1983; Woffinden and Murphy 1983; González et al. 1985). Imitation of adult hunting maneuvers, also observed in other raptors (Ficken 1977; Paull 1977; Bildstein 1980; Johnson 1986), can be considered a form of play that helps with development and training of muscles used during hunting (Bekoff 1976; Fagen 1976). We do not believe these behaviors correspond to failure at catching prey, since we did not see juveniles capture prey during observations.

As in other raptors (see Mueller and Meyer 1985), the different behaviour of both adults suggests that the parental role of each sex was different. The smaller adult "B," probably the male, was mainly hunting and bringing prey to the young, while adult "A," probably the female, defended the nest area.

Apparent aggression of adults towards young may be related to the development of juvenile flight and/or to dispersal (Brown and Amadon 1968; Trivers 1974; Milburn 1979; Sherrod 1983). In this last sense aggression can be interpreted as a behavior directed to chase offspring off the adults' hunting ground (Alonso et al. 1987). Adult-juvenile and juvenile-juvenile aggressive interactions may indicate increasing tensions among family members as adult care of young decreases, as expected in parent-offspring conflict prior to family rupture (Trivers 1974). Juveniles, however, seemed to demand the same degree of attention from parents throughout the ob-

servation period. On the other hand, as our data might suggest and for some raptors living in temperate climates (Alonso et al. 1987), the dispersal of a *Buteo albonotatus* family group is initiated by the parents. Obviously, our results should be considered as preliminary, since our reported observations are based upon a single pair. No evidence exists to support the idea that juveniles actually separated from adults during the observation period. The family may have remained together away from the nest area, as probably occurs with other congeneric species (Johnson 1986).

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New England Hawk Watch Conference. The New England Hawk Watch will hold a one day conference on subjects related to raptors and raptor migration. The conference will be held on Saturday, 7 April 1990, at the Holiday Inn in Holyoke, Massachusetts (site of previous NEHW conferences). The program is presently in the planning stage. Following the day's events, there will be a banquet with Peter Dunne as guest speaker. **For more detailed information and pre-registration write to: HAWKS, P. O. Box 212, Portland, Connecticut 06480 USA.**

SHORT COMMUNICATIONS

EGGS OF CAPTIVE CRESTED EAGLES (*Morphnus guianensis*)

LLOYD F. KIFF, MICHAEL P. WALLACE AND NATHAN B. GALE

Little is known of the breeding habits of larger Neotropical eagles, including the widespread Crested Eagle (*Morphnus guianensis*), and we are unaware of any published descriptions of the nest and eggs of the species. Bierregard's (*Wilson Bull.* 96(1):1-5, 1984) report of a nest in Manaus, Brazil is apparently the only published nesting account for this species. Kreuger (*Oologists' Rec.* 43:5-6, 1963) described a purported Crested Eagle egg from his collection, but we have doubts about the authenticity of the specimen. Therefore, we include herein descriptions of eggs laid by 2 Crested Eagles in captivity.

Three eggs (West. Found. Vert. Zool. Nos. 156,586-8) laid on 18 January, 27 January, and 25 February 1988, respectively, by a Crested Eagle housed at the Los Angeles Zoo are dull white in color, unmarked (aside from heavy dark brown nest stains), short subelliptical in shape (Preston In Palmer, *Handbook of North American birds*, vol. 1, Yale Univ. Press, New Haven, Connecticut, 1962) and measure 57.5 × 43.9, 55.5 × 42.7, and 51.8 × 41.2 mm, respectively. Corresponding empty shell weight (g) and shell thickness (measured at middle latitudes of the eggs;

given in parentheses in mm) are 7.215 (0.598), 6.738 (0.556), and 5.953 (0.552).

The female was obtained as a recent fledgling from local Indians in Depto Amazonas, northeastern Peru in early 1978 (J. P. O'Neill, pers. comm.). The female was housed from 28 March 1978-10 November 1987 at the Oklahoma City Zoo, where she laid a minimum of 25 eggs between August 1982 (at an age of 5 yrs)-February 1986 (T. Todd, in litt.). In 8 instances a second egg was laid from 3-10 days ($\bar{x} = 7.4$) after a first egg, suggesting that a clutch size of 2 eggs may be typical of this species. The nest studied by Bierregard (1984) also contained two eggs. Although the bird has been housed with a male throughout her captive life, all eggs laid have apparently been infertile.

A single egg (West. Found. Vert. Zool. No. 156,276) laid by another female at the Center for Propagation of Endangered Panamanian Species (CEPEPE), Balboa, Republic of Panama, is also dull white, unmarked, short subelliptical in shape, and measures 64.0 × 50.7 mm; empty shell weight is 7.614 g, and shell thickness at the larger end is 0.565 mm. That female was 5 yrs old when the egg was laid, and she has been producing eggs since she was 2 yrs old. She was obtained from the wild at the time of her apparent first flight near a nest site on Rio Chiquita Ridge, central Panama. The bird is presently housed with a younger male, but no fertile eggs have been produced.

Eggs of the Los Angeles female are markedly smaller than eggs from the Panamanian bird (Fig. 1). Weights of the 3 Los Angeles eggs taken within 2-3 d after laying were 60.3, 55.7, and 46.3 g, respectively ($\bar{x} = 54.1$ g). Based on the equation of Hoyt (*Auk* 96(1):73-77, 1979), fresh weights of the same eggs were 60.9, 55.7, and 48.4 g for an average of 55.0 g, representing only 1.9% of the Los Angeles female's body weight (2950 g). Doubtless, a 55.0 g egg is an atypically small weight for the species, and unusually small egg size has been noted in the eggs of other captive bird species, including raptors (T. Cade, pers. comm.; B. Walton, pers. comm.). The egg of the Panamanian bird had a calculated fresh weight of 90.5 g, or 3.1% of body weight (2950 g), which is presumably nearer to the expected egg weight, judging from other large eagles, including *Aquila* and *Haliaeetus* (Schonwetter, M. *Handbuch der Oologie*, vol. 1. Akademie Verlag, 1967). Color, texture, and shape of the eggs closely resemble those of the larger Harpy Eagle (*Harpyia harpyja*). The egg reported by Kreuger (1963) measured 73.7 × 53.4 mm (calculated whole wt = 107.2) and was described as "deep cream with large pale yellow-brown spots, richly dispersed round the larger end of the egg, with finer small spots spread over the rest of the surface," thus differing mark-



Figure 1. Eggs laid by captive Crested Eagles. Panama (top); Los Angeles Zoo (bottom).

edly in both color and size from the captive-laid eggs described here.

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We thank Jon Fisher and Dana Gardner for various forms of assistance and Clark Sumida for preparing the Los Angeles eggs, measuring their thickness, and preparing Fig. 1. John O'Neill and Trey Todd provided details on the history of the female now at the Los Angeles Zoo. This note was supported by the Western Foundation of Vertebrate Zoology.

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SERUM ESTRADIOL-17 β AND TESTOSTERONE LEVELS IN GREAT HORNED OWLS (*Bubo virginianus*)

SUSAN A. MAINKA, GEORGE J. HALMAZNA AND LORI M. ROGERS

Reproductive hormone levels of raptors have been studied in the American Kestrel (*Falco sparverius*) (Rehder et al., *Steroids* 43(4):371-383, 1984). This study was designed to provide information about estradiol-17 β and

testosterone levels in the Great Horned Owl (*Bubo virginianus*) and also to determine the effect of the presence of both male and female on the other sex during the breeding season.

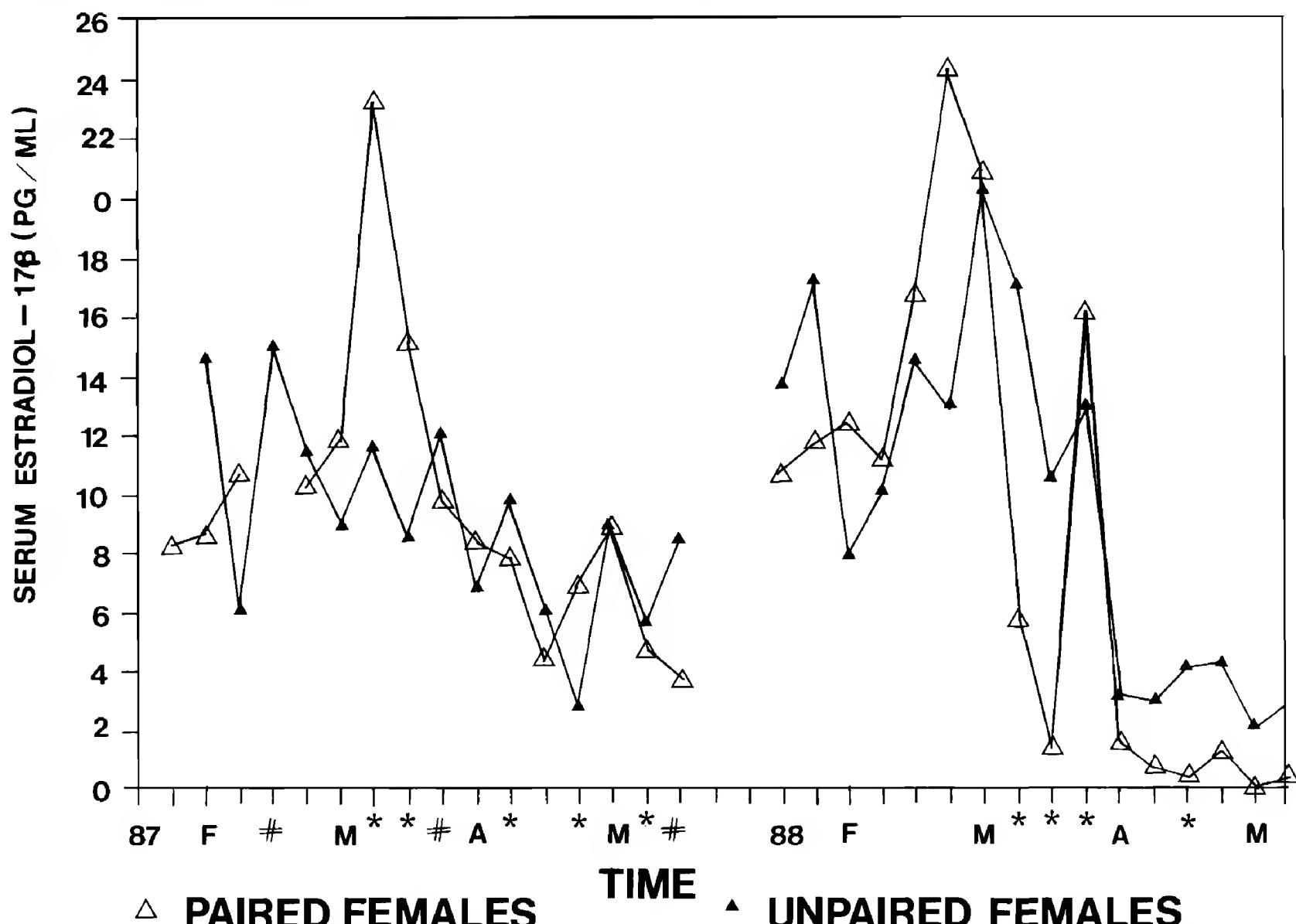


Figure 1. Serum estradiol-17 β levels measured in paired female Great Horned Owls ($N = 2$) and unpaired female Great Horned Owls ($N = 3$ in 1987, $N = 5$ in 1988). Values given are mean values for each sample date in pg/ml. (nb * $N = 1$ paired bird, # $N = 1$ unpaired bird)

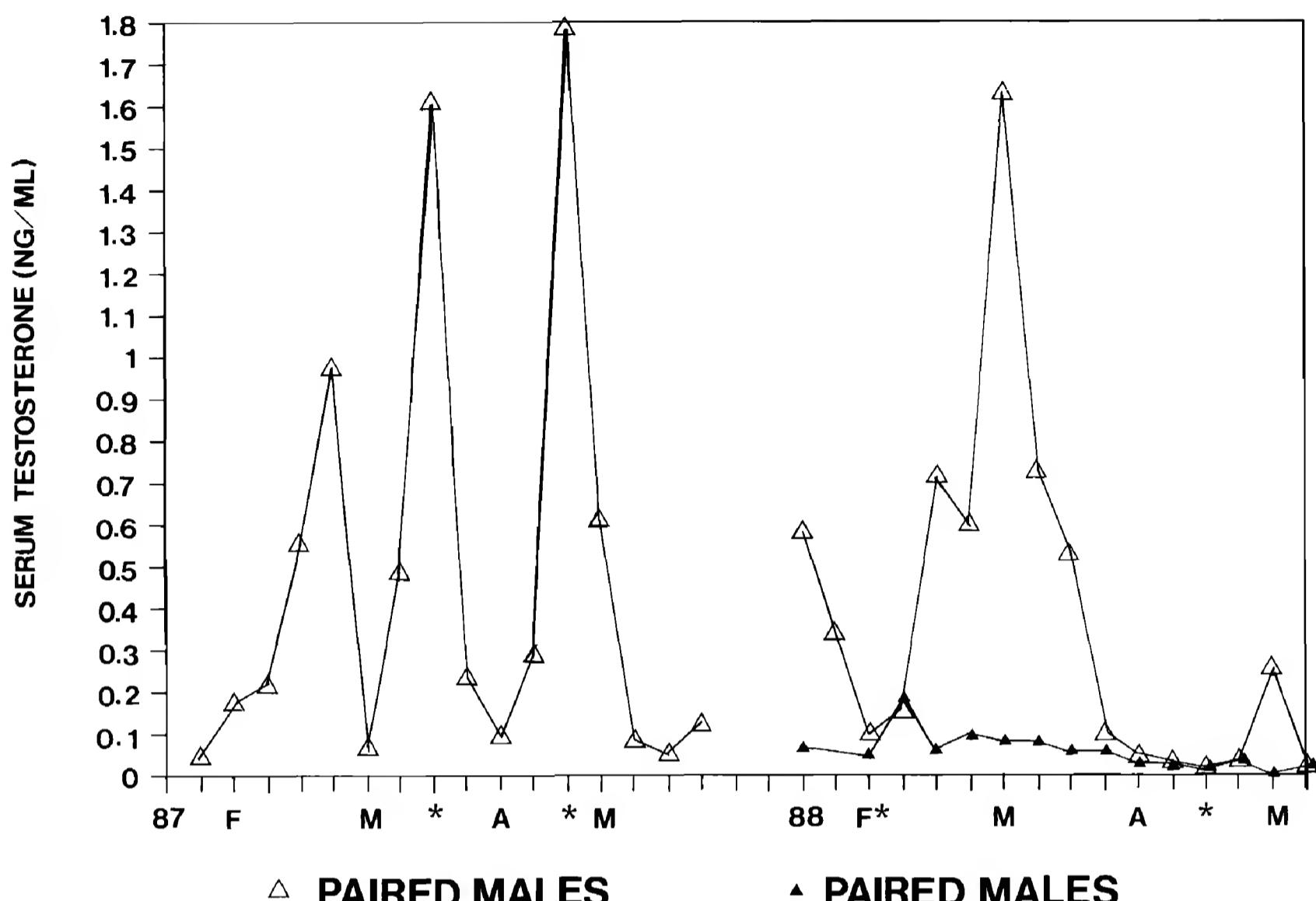


Figure 2. Serum testosterone levels measured in paired male Great Horned Owls ($N = 2$) and in 1 unpaired male Great Horned Owl (in 1988). Values given for paired males are mean values in ng/ml. (nb * $N = 1$)

A total of 11 Great Horned Owls were used in this study, 7 birds in 1987 and 10 birds in 1988, 6 of which were part of the 1987 sample group. Each bird was presented to the Calgary Zoo as injured wildlife and was medically and/or surgically treated. Birds were fully recovered from any injuries and had been part of the zoo collection for at least 2 mo prior to the beginning of the study. All birds were fed day-old chicks with vitamin/mineral supplementation (SA-37, Rogar STB, London, Ontario, N6A 4C6). The birds were all housed in outdoor enclosures and were therefore exposed to natural photoperiod and outdoor temperatures.

Each bird was laparoscopically sexed then placed into 1 of 2 groups; females only or male/female pairs. Females were housed in groups of 2 or 3 and each of 2 pairs was housed separately. A single male, housed separately, was added to the study during the second year.

Blood samples were collected weekly from all birds from January to May in 1987 ($N = 7$) and 1988 ($N = 10$). Two to 3 ml were taken from the brachial vein and placed in a serum tube for centrifugation. Serum was separated and frozen, and the samples were submitted to the reproductive physiology lab at the Western College of Veteri-

nary Medicine, Saskatoon, Saskatchewan for assay. Samples from females were analyzed for estradiol- 17β by radioimmunoassay following the method of Rawlings et al. (*Theriogenology* 22:473-488, 1984). Samples from males were analyzed for testosterone by radioimmunoassay according to the method of Cook et al. (*Steroids* 40(4):369-380, 1982). Data was not obtained from all birds at all sampling dates, either due to inability to obtain a sample or due to insufficient sample size. Therefore, no statistical comparison of paired versus unpaired data was done.

During the sampling period, no copulatory behaviour was seen in any of the paired owls and no eggs were laid. One of the pairs being used in the study functioned as foster parents to nestling owls which are presented to the zoo for care. The level of individual bird's estradiol- 17β peak in 1987 ranged from 12.5-23.3 pg/ml in paired females ($N = 2$) and from 12.2-26.5 pg/ml in unpaired females ($N = 3$). In 1988 individual estradiol- 17β peaks in paired females ($N = 2$) ranged from 14-39.5 pg/ml and in unpaired females ($N = 6$) ranged from 21.8-32.1 pg/ml. Mean serum estradiol- 17β levels in paired females peaked in early March in both 1987 and 1988. Unpaired females showed no definite peak in 1987 but did have an

elevation in serum estradiol-17 β in early March of 1988 (Fig. 1). Levels of estradiol-17 β in both groups appeared to be higher in 1988 compared to 1987 (Fig. 1).

In both years the peaks in estradiol-17 β occurred in all individuals in mid-February to mid-March. Breeding season for Great Horned Owls is January–March while for kestrels is April–May (Bent, *Life histories of North American birds of prey*. Dover Publications Inc. New York, 1938).

Estradiol-17 β levels measured in this study are lower than those recorded by Rehder et al. in egg-laying female American Kestrels. Estradiol-17 β levels in those kestrels in February were 74.5 pg/ml. The kestrels were reproductively active (egg-laying) while owls in this study showed no reproductive behaviours and, although no reproductive activity was seen during the study, this is the period during which estradiol-17 β peaks occurred in females in this study.

Testosterone levels between the paired males and one unpaired male in this study were notably different (Fig. 2). The unpaired male showed little variation from a level of 0.05–0.1 ng/ml while the paired males appeared to "cycle" at monthly intervals with mean peak serum testosterone levels of 1–2 ng/ml. Unfortunately, only 1 male

was unpaired and a larger number of birds would be needed to help determine the validity of these results.

Under the conditions in this study, the levels of estradiol-17 β measured in paired and unpaired female Great Horned Owls was lower than levels seen in egg laying American Kestrel females. While the female Great Horned Owls in this study did not seem to need the presence of a male to show some reproductive hormone activity, results seen with 1 unpaired male may indicate that the male may require the presence of a female to cause increases in serum testosterone. A larger sample size would be needed for confirmation.

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CHANGES IN WINTER DISTRIBUTION OF BALD EAGLES ALONG THE COLORADO RIVER IN GRAND CANYON, ARIZONA

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AND JOHN WEISHEIT

Distribution of wintering Bald Eagles (*Haliaeetus leucocephalus*) in the continental United States has been greatly influenced by construction and operation of dams and reservoirs (Stalmaster 1987). In contrast to reservoir-induced destruction of riverine habitats on which many wintering Bald Eagles have relied, some dams and reservoirs may harbor alternative or new food sources. Eagles may congregate below some dams in winter to feed on fish that are killed or stunned while passing through turbines, or to hunt in ice-free water immediately below other dams (Southern 1963; Spencer 1976; Steenhof 1978). Other riverine phenomena, such as salmonid spawning runs, may influence wintering Bald Eagles to congregate (Servheen 1975; Stalmaster 1976). In Glacier National Park, Montana, introduced Kokanee Salmon (*Oncorhynchus nerka*) have attracted the densest concentration of migrating Bald Eagles in the continental United States (McClelland et al. 1982).

In this study, we document how operation of Glen Canyon Dam and a run of introduced Rainbow Trout (*Salmo gairdneri*) have changed the abundance and distribution of wintering Bald Eagles along the Colorado River in Grand Canyon National Park, Arizona.

The study area encompassed a 386 km segment of the Colorado River from Glen Canyon Dam to Diamond Creek, Arizona. Completion of Glen Canyon Dam on the Colorado River near Page, Arizona, greatly altered downstream river characteristics through Grand Canyon National Park (Turner and Karpiscak 1980; Howard and Dolan 1981). Average annual maximum flows were reduced from 2438 cubic m/sec (cms) to 790 cms, and median discharge was increased to 360 cms. Average diurnal fluctuation in river stage was increased from a few centimeters to several meters; median sediment concentrations were reduced from 1500 to 7 parts per million. Average annual water temp was reduced from a range of 0.2°–28°C during

the pre-impoundment period (1949–1962), to a range of 5.5°–18°C during the 1963–1976 post-impoundment period (Turner and Karpiscak 1980). Completion of the dam changed the Colorado River from a turbid, seasonally variable stream supporting a native, warm-water fishery into a clear, relatively non-fluctuating stream supporting a largely non-native, cold-water fishery (Johnson and Carothers 1987).

Dominant native fishes of the pre-impoundment river, including Bonytail (*Gila elegans*), Humpback Chub (*G. cypha*), Roundtail Chub (*G. robusta*), Colorado Squawfish (*Ptychocheilus lucius*), and others, were extirpated or reduced in numbers following impoundment, and introduced Rainbow Trout and Common Carp (*Cyprinus carpio*) began to dominate the fishery after 1963 (Johnson and Carothers 1987). Trout had been introduced into several Colorado River tributaries in Grand Canyon prior to 1963, but colonization was limited in the mainstream; trout quickly colonized the river after impoundment, both from tributaries and from Arizona Game and Fish Department stocking efforts below Glen Canyon Dam (Maddux et al. 1987).

In the mid-1970s spawning Rainbow Trout were first observed in Nankoweap Creek, a small tributary to the Colorado River 110 km downstream from Glen Canyon Dam. Trout had never been introduced directly into the creek. By the mid-1980s as many as 1500 spawning Rainbow Trout were present in the lowermost 1.5 km of the creek on peak days during the spawn, which lasted from November through April (H. Maddux and D. Kubly, pers. comm.).

Nankoweap Creek is an 84.4 km² drainage arising on the North Rim of the Grand Canyon, flowing 14 km to its confluence with the Colorado River (Webb et al. 1987). The creek is fed by perennial springs and runoff from the Kaibab Plateau. Annual flows range from 0–1.09 cms (Johnson and Sanderson 1968), but winter flows typically range from ca. 0.05–0.20 cms.

We surveyed the study area for wintering Bald Eagles 8 times from March 1987 to April 1988 (Fig. 1). Approximately 20–25 km/d were surveyed from boats as we floated downstream on each of 5 boat surveys; 1–7 d were also spent at the mouth of Nankoweap Creek on each survey. Three rim surveys of the Nankoweap Creek area were made from a fixed point on the canyon rim within the Navajo Indian Reservation using spotting scopes. Individual eagles may have been counted more than once during downriver surveys due to the number of days of each and the fact that individual eagles could easily have flown from one survey area to the next in a day. Count data from fixed points at or near the mouth of Nankoweap Creek listed in Figure 1 were taken from the greatest number of adults or subadults seen at one time on any given day. Numbers of trout in the lowermost 0.65 km of Nankoweap Creek were counted on each visit to that site. Historical information on eagle presence in the study area

was obtained from river surveys by Carothers and Aitchison (1976) and by D. H. Ellis (pers. comm.), and from helicopter surveys by the Navajo Fish and Wildlife Department (unpubl. report, Windowrock, Arizona).

The known occurrence of Bald Eagles in the study area is summarized in Figure 1. Abundance and distribution of wintering Bald Eagles along the Colorado River in Grand Canyon was unknown before 1963; however, post-impoundment winter surveys for Bald Eagles suggest that eagles were not present immediately after construction of the dam.

Wintering Bald Eagles have increased in numbers along the Colorado River in Grand Canyon, evidently in response to trout availability in Nankoweap Creek and in the river. Regulated discharge from Glen Canyon Dam apparently induced these changes. The mouth of Nankoweap Creek was a concentration point for eagle activity due to apparent ease with which eagles could forage on spawning trout in the shallow, exposed creek channel, but eagles were also found in other areas above confluence of the Little Colorado River.

Spawning trout were observed in Nankoweap Creek from December 1987–April 1988, with one or more peaks of spawning between January and March 1988. Adult trout densities ranged from 54–457 individuals in the lowermost 0.65 km of the creek, with increasing abundance of trout fry through April. Spawning trout averaged 41 cm in length (N = 30; S.E. = 1.19 cm). Prey captures of live trout (no dead trout were seen during the study period) were observed (N = 7) in the lowermost 0.3 km of the creek and at the confluence of the river and the creek. Bald Eagles were present at the mouth of Nankoweap Creek only when spawning trout were present; the known peak of eagle occurrence (18 individuals in February 1988) coincided with the approximate peak of the trout spawn.

Development of a concentration of wintering Bald Eagles at Nankoweap Creek in Grand Canyon is similar to the increase in eagle abundance documented at McDonald Creek in Glacier National Park, Montana (McClelland 1973). Kokanee Salmon were introduced into McDonald Creek in 1916, and annual autumn spawning eventually attracted large numbers of migrating Bald Eagles which formerly had been uncommon (McClelland 1973).

Increase in eagle abundance at Nankoweap Creek in Grand Canyon is of management concern to both the Bureau of Reclamation (which manages water released from the dam) and the National Park Service (which manages recreational use of Nankoweap Creek). Low water levels released from the dam in winter can seriously impair trout spawning (Maddux et al. 1987), and therefore the eagle prey base. The National Park Service is under steady pressure to allow greatly increased recreational fishing use of Nankoweap Creek to exploit the newly-developed trout spawn, a potential source of disturbance to the eagles (Stalmaster and Newman 1978). Bright Angel and Tappat creeks (ca. 60 and 150 km downstream, respectively)

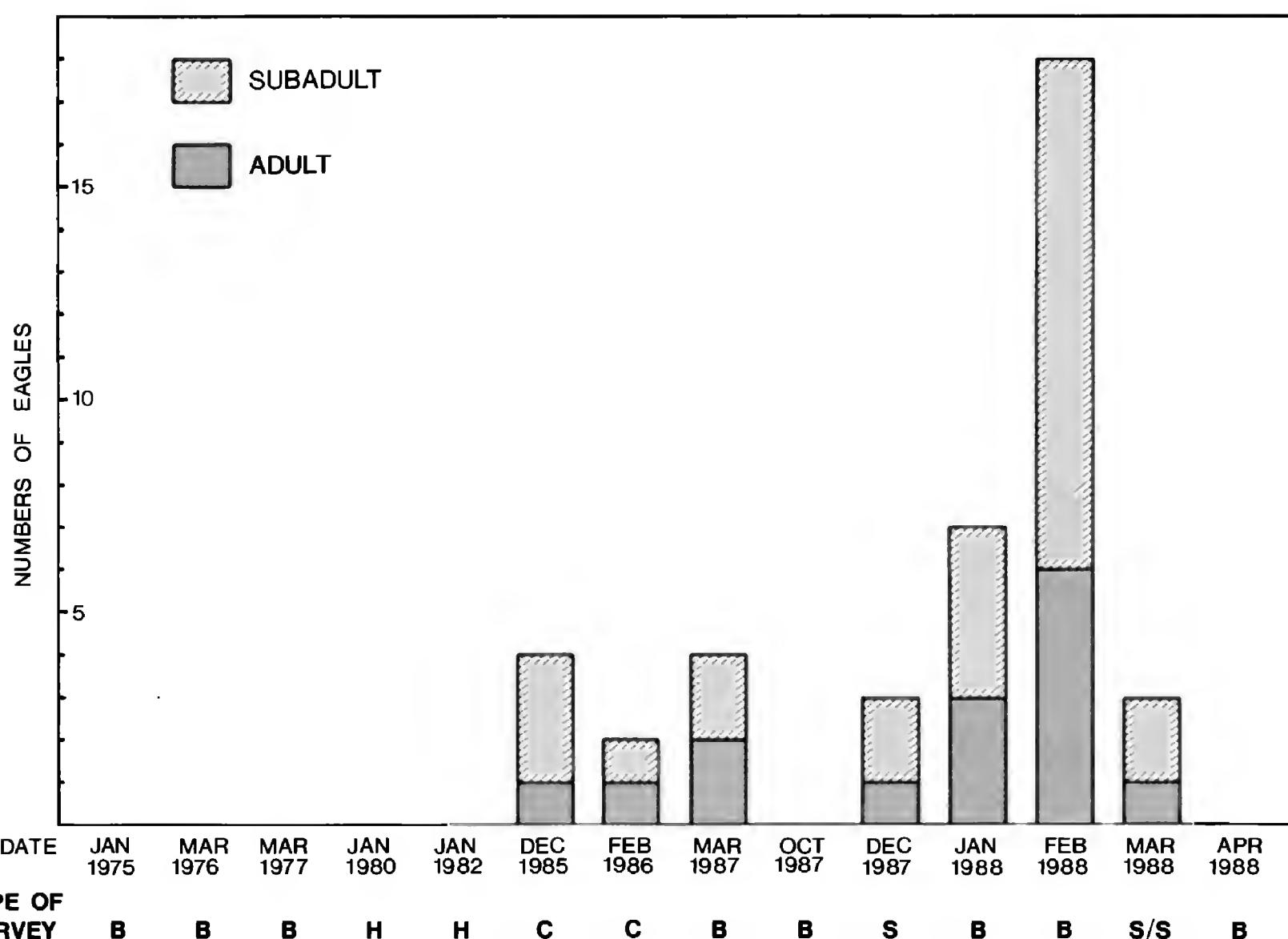


Figure 1. Occurrence of wintering Bald Eagles along the Colorado River in Grand Canyon National Park, Arizona, 1975–1988. Types of eagle surveys include: B = 18-d boat survey of entire river corridor; H = 1-d helicopter survey of upper third of study area (Glen Canyon Dam to Little Colorado River; 123 km); C = casual observations by biologists at the mouth of Nankoweap Creek; S = 1-d survey of mouth of Nankoweap Creek from canyon rim using spotting scope.

also support sizeable trout spawns along this section of river, but other factors may preclude their usefulness as alternative eagle foraging areas. Bright Angel Creek is the site of an intense recreational development, while Tapeats Creek enters the river in an extremely narrow bedrock gorge where spawning trout would be less accessible to foraging eagles.

Although the regional abundance of wintering Bald Eagles may vary annually, the 18 eagles at Nankoweap in February 1988 represented ca. 20% of the total statewide wintering population (Grubb and Kennedy 1982). Annual abundance of spawning trout at Nankoweap Creek and their accessibility to foraging eagles suggest future increases in the number of Bald Eagles there as the regional wintering population becomes aware of and habituated to this new food resource.

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EGG MEASUREMENTS FROM A NORTHERN GOSHAWK
(Accipiter gentilis gentilis) INCLUDING ONE ABNORMALLY LARGE EGG WITH
TWIN EMBRYOS

S. J. PETTY AND D. I. K. ANDERSON

Twin embryos are rare in the eggs of wild birds (O'Conner 1984). In captive birds the incidence of twinning has been experimentally increased in the Mallard (*Anas platyrhynchos*) by keeping the eggs at low temp prior to incubation (Batt et al. 1975) and in Domestic Chickens (*Gallus gallus*) by exposing laying females to temps inducing hypothermia (Sturkie 1946). Romanoff and Romanoff (1949) considered that double yolks were not unusual in Domestic

Chickens although single yolked eggs with 2 blastoderms were very rare. We can find only 1 published account of twin embryos in the egg of a raptor, namely a Peregrine (*Falco peregrinus*) from Greenland (Pattee et al. 1984).

As part of a population study of the Northern Goshawk (*Accipiter gentilis gentilis*) in Great Britain we visited a nest on 5 May 1988 and noted 1 very large egg amongst a clutch of 3 fresh eggs. The largest egg was the dirtiest,

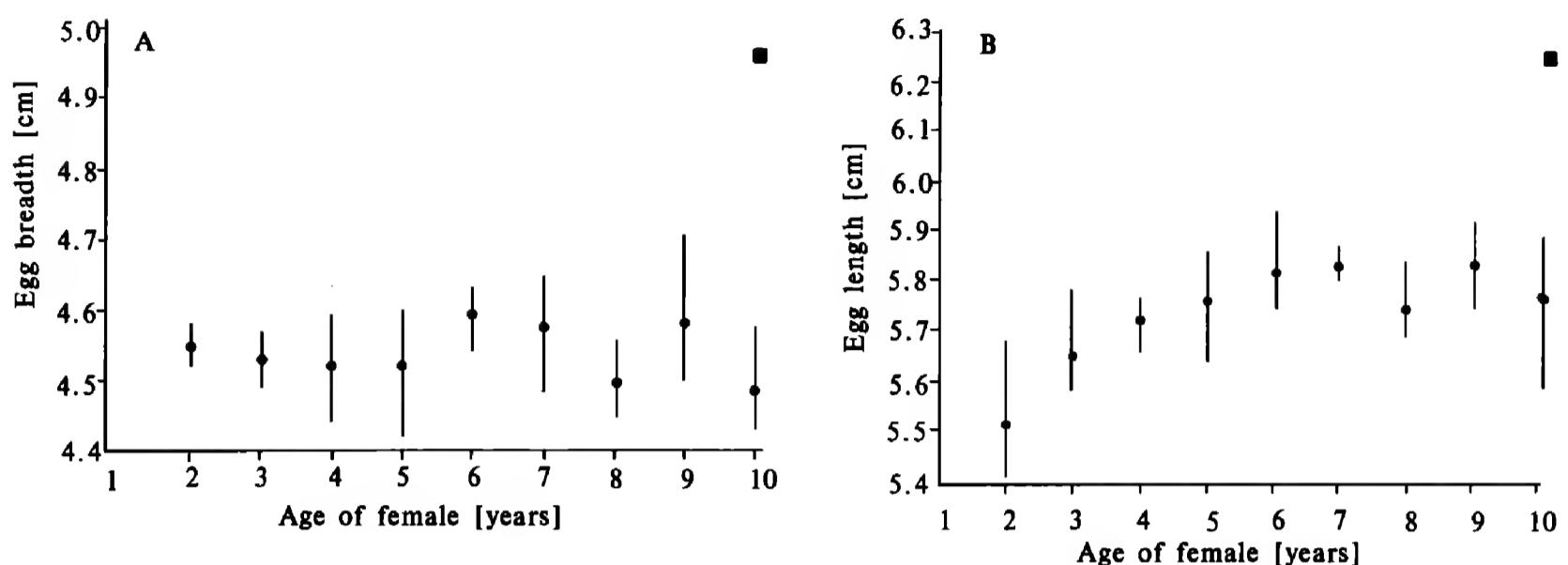


Figure 1. The breadth (A) and length (B) of eggs laid by 1 female Northern Goshawk between the ages of 2 and 10. Circles give the means for each clutch; endpoints of bars show the maximum and minimum within a clutch. The square indicates the abnormal egg.

Table 1. Reproductive history and egg biometrics (cm) of 1 female Northern Goshawk from age 2 to 10. The bird also bred as a yearling in 1979 and reared 2 chicks but eggs were not measured.

YEAR	FEMALE AGE	CLUTCH SIZE	BROOD SIZE ^a	EGG BIOMETRICS		
				LENGTH \pm S.D. (RANGE)	BREADTH ^b \pm 1 S.D. (RANGE)	VOLUME INDEX ^c \pm 1 S.D. (RANGE)
1980	2	3	2	5.52 \pm 0.14 (5.41–5.68)	4.55 \pm 0.03 (4.52–4.58)	114.26 \pm 2.06 (112.00–116.04)
1981	3	4	0	5.65 \pm 0.09 (5.58–5.78)	4.53 \pm 0.03 (4.49–4.55)	115.63 \pm 0.70 (114.82–116.53)
1982	4	4	4	5.72 \pm 0.05 (5.66–5.77)	4.52 \pm 0.07 (4.44–4.59)	117.02 \pm 4.05 (111.58–120.51)
1983	5	3	2	5.76 \pm 0.11 (5.64–5.86)	4.52 \pm 0.08 (4.42–4.57)	117.58 \pm 6.43 (110.19–121.85)
1984	6	3	2	5.82 \pm 0.11 (5.75–5.94)	4.59 \pm 0.05 (4.54–4.63)	122.52 \pm 0.69 (121.88–123.26)
1985	7	4	4	5.83 \pm 0.04 (5.80–5.87)	4.57 \pm 0.08 (4.48–4.61)	121.51 \pm 3.21 (117.81–123.47)
1986	8	3	3	5.75 \pm 0.06 (5.69–5.79)	4.49 \pm 0.06 (4.45–4.56)	115.8 \pm 2.17 (114.46–118.32)
1987	9	4	2	5.83 \pm 0.09 (5.75–5.92)	4.57 \pm 0.09 (4.49–4.70)	121.96 \pm 4.23 (118.52–127.46)
1988	10	4	0	5.77 \pm 0.16 (5.59–5.89)	4.48 \pm 0.08 (4.43–4.57)	115.95 \pm 5.44 (110.70–121.55)
1988 abnormal egg				6.25	4.96	153.76

^a Number of chicks leaving the nest.

^b Measured at the widest point.

^c Volume index = $L \times B^2$, when L = length and B = breadth.

suggesting that it was the first laid. Two days later 1 additional normal-sized egg was present in the nest. We found the nest freshly deserted on 10 June with 2 dead chicks and 2 addled eggs, including the large one. One chick was about 3 d old and the other <1 d old, and the last laid egg was just starting to hatch. Both eggs were removed under licence.

Moulted primary feathers were collected annually and used to identify the adults (Opdam and Muskens 1976). We knew the complete reproductive history of this particular female. She first bred as a yearling in 1979 with a 2 yr-old male. She kept the same mate, and the pair used the same nesting territory for each of 10 breeding attempts during 1979–1988. Each year, except for 1979, we measured length and breadth of each egg to the nearest 0.01 cm. Egg breadth showed no trend with age of the female (Fig. 1A), unlike egg length which increased to a plateau at around 3–4 years of age (Fig. 1B). Length and breadth of the abnormally large egg collected in 1988 was well outside the range of all other eggs laid by this female (Fig. 1); volume index of 153.76 cm³ was 20.6% greater than the next largest egg with an index of 127.46 cm³ (Table 1), and fresh laid weight was 82.6 g compared to 63.0 ± 3.10 g (mean \pm 1 S.D.) for other eggs in the same clutch.

The large egg was opened in October 1988 and 2 embryos of a similar size (about 10–15 d old) in 1 yolk sac were discovered. Incubation period in Northern Goshawks is around 35–38 d (Cramp and Simmons 1980). Embryos were partly decomposed and appeared to have died prior to the nest being deserted because far less development was evident than those in the other eggs.

Pattee et al. (1984) gave no data on normal egg sizes laid by the Peregrine which produced twin embryos but did show that the egg was considerably longer and wider than other Peregrine eggs collected for pesticide analysis from the same area. Our observations show that with the same female Northern Goshawk, the egg with twin embryos was considerably larger than normal. This female was one of the oldest in our study population. She was also one of the most successful, having produced 21 chicks during her lifetime (Table 1). To desert when the chicks

were hatching suggests that she may also have been under stress throughout the breeding attempt. We have measured over 400 eggs from other Northern Goshawks during the same period and in the same area, and none were found to be so large. However, giant eggs do occur in other species. In a sample of 200,000 Domestic Chicken eggs, 89 were unusually large (Romanoff and Romanoff 1949). Whatever the cause for twinning, the phenomenon appears to be an extremely rare occurrence in the Northern Goshawk.

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UNUSUAL ROOST SITE SELECTION AND STAGING BEHAVIOR OF BLACK-SHOULDERED KITES

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Communal night roosting in winter has been reported in the North American race of the Black-shouldered Kite (*Elanus caeruleus leucurus*) (Dixon et al. 1957; Bolander and Arnold 1965; Waian and Stendall 1970), as well as for the nominate race (*E. c. caeruleus*) (Cramp and Simmons 1980; Brown et al. 1982). Kites are almost always reported to roost in trees of various species, but Mendelsohn (1988) reported several accounts of kites roosting in reed beds in Africa. Kites coming in to roost usually stage in nearby trees, flying from tree to tree as they approach the roost site. Thus, it was with great interest that we observed over 100 Black-shouldered Kites forming a night roost in a field of sugar cane; many were staging by perching as a group on the ground in a nearby plowed field.

On 20 December 1987 in the late afternoon, we observed a handful of Black-shouldered Kites, all flying purposefully but individually, in the same direction. We followed to locate the presumed roosting area. The birds we followed joined others that were perched close together on the ground in a recently plowed field; the bunch appearing somewhat like a flock of gulls. We counted up to 32 individuals on the ground at one time. While observing these birds, another 30 to 35 flew up from a large (approx. 300 m × 500 m) sugar cane field directly behind us; the latter group milled around in the air for approximately 10 min, then gradually settled back in the cane field; sugar cane plants were 4–5 m in height. As darkness approached, ground-perching kites flew individually to positions above the sugar cane and dropped in, presumably to roost for the night. Just after sunset, most of the kites flew from the cane field and milled around in the air. At that time we estimated over 100 individuals; eventually all again settled back into the cane field. In the late afternoon of 25 December WSC returned to the area to further observe staging and roosting behavior. A maximum of 65 staging kites were perched on the ground at one time in the same area. As darkness approached, each flew into the sugar cane field and roosted as described above. Again, an estimate just before dark of milling kites was >100 individuals. The sugar cane field was located approximately 1 km northwest of the town of Madero, Texas, just north of the Mexican border and about 5 km from Bentsen State Park, where we first observed kites flying to the roost area.

Late in the afternoon of 28 December 1988 WSC followed 4 kites flying north from the Santa Ana National

Wildlife Refuge (approximately 30 km east of the roost area described above) for about 3 km to where each settled into a small (approximately 100 m × 300 m) sugar cane field. Several other kites were seen hovering nearby.

Donahue (Lasley 1986) reported a [night] roost of 79 kites in a [sugar] cane field on 30 December 1985 near the same area without comment; the only reference, to our knowledge, of Black-shouldered Kites roosting communally in anything other than trees in North America. However Bloom (pers. comm.) has several times seen approximately 30 birds roosting 1 m above the ground on dead artichoke thistle flower stalks in California. Groves of large trees were seen within sight of the sugar cane field; the lack of suitable trees can be ruled out as the reason for this choice of roost site.

The number of kites in most reported roosts is typically in the tens, with numbers over 100 rare (Bolander and Arnold (1965) counted 156, and Bloom (pers. comm.) counted 194, both in California). Cramp and Simmons (1980) mention that the usual number per roost for the nominate race is 10–20, sometimes up to 100, rarely 500. On this basis, our sugar cane night roost attracted a greater than usual number of kites. Further, staging behavior in the form of communal ground roosting has been not reported previously for Black-shouldered Kites.

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THE BARTOS TRAP: A NEW RAPTOR TRAP

ROBERT BARTOS, PENNY OLSEN AND JERRY OLSEN

Many effective means of live trapping birds of prey are available, including bal-chatri [Berger, D. D. and H. C. Mueller. 1959. The Bal-Chatri: A trap for birds of prey. *Bird Banding* 30:18-26; Olsen, J. and P. Woppard. 1975. The use of the bal-chatri in banding. *Canberra Bird Notes* 3(4):8-9], noose carpet, mist net and dho-gazza (e.g., Beebe, F. L. and H. M. Webster. 1964. North American falconry

and hunting hawks. World Press, Colorado), Swedish Goshawk trap (e.g., Beebe and Webster 1964) and its derivatives, and "flip trap" [e.g., Cam-Hardy universal raptor trap, Cam. G. R. 1985. A universal raptor trap. *Corella* 9(2):55-58]. The most appropriate trap will depend upon target species and circumstances. Sometimes setting a variety of traps is useful to increase the chances

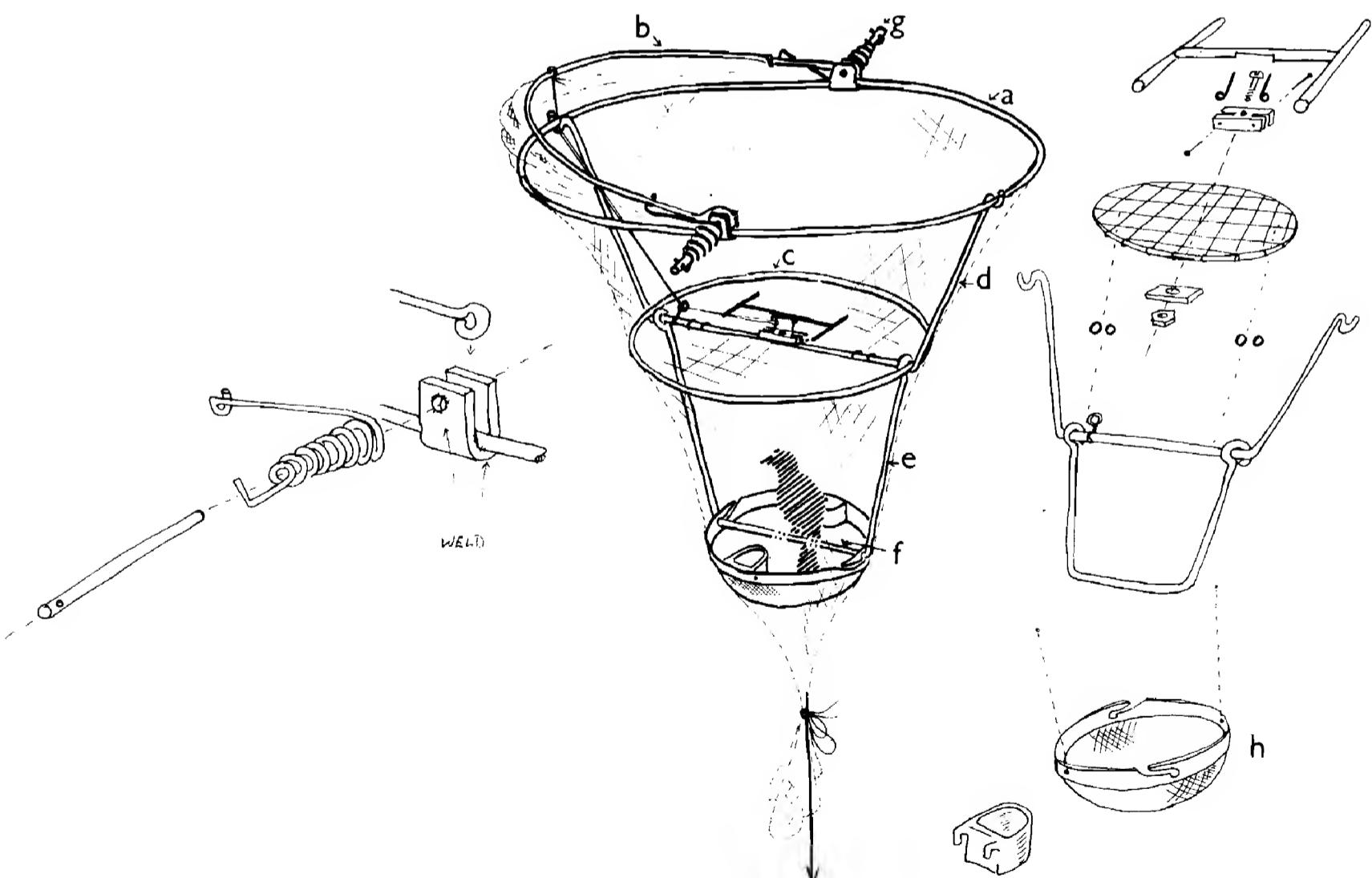


Figure 1. Assembly instructions for the Bartos Trap.

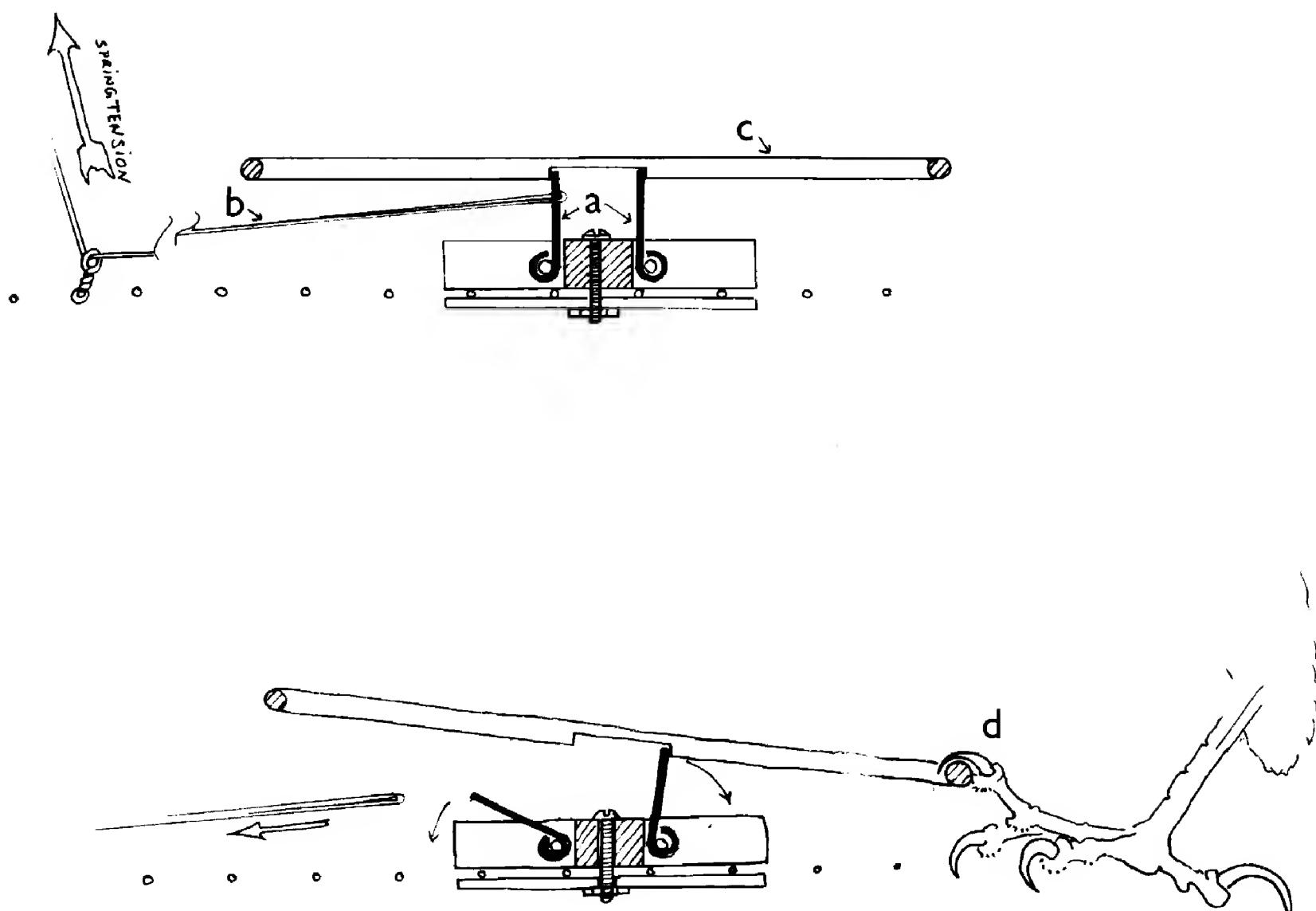


Figure 2. Assembly instructions for trigger mechanism.

of capturing a particular raptor, or, when recapture is necessary, to overcome the problem of avoidance of a type of trap in which the raptor has already been captured.

Here we report on a versatile and convenient new trap, designed by Robert Bartos, which has several unique characteristics. The Bartos Trap can be suspended at almost any height (e.g., in a building or in a tree near a nest), to capture species reluctant to venture to the ground. Once captured the raptor is enclosed: unlikely to injure itself and safe from predators. The trap need not be attended and thus has several advantages over a mist net type of trap. When assembled in alternative form and set on the ground, the trap is similar to the "flip trap" (see above). Further, the trap can be collapsed flat for easy carrying.

So far we have used the trap to capture only 2 particular individual raptors: a Collared Sparrowhawk (*Accipiter cirrocephalus*) unable to escape from a warehouse and a Boobook Owl (*Ninox novaeseelandiae*) in a wooded paddock, recaptured for removal of a radio transmitter. In both cases the trap was left and the raptor captured on our return about 2 hr later. We have also caught Kookaburras (*Dacelo gigas*) and Pied Currawongs (*Strepera graculina*), and, with a sparrow as a lure and the trigger set fine, House Sparrows (*Passer domesticus*).

Trap Construction. The main ring (Fig. 1a), bow arm (Fig. 1b), and divider frame (Fig. 1c) are made from soldered metal rod approximately 4 mm dia. Remaining sections of the frame are heavy gauge wire (approximately 10-12 gauge). An inexpensive fishing scoop net (black tetron or similar) forms separate netting compartments for raptor and lure. The net's diameter at full stretch determines the size of the elliptical main ring (in our trap about 62 cm \times 57 cm) and bow arm. In our trap the divider is about 33 cm dia, the spreader arms (Fig. 1d) 21 cm long, and the length of the swing for the lure compartment 12 cm (Fig. 1e) and lure perch (Fig. 1f) 21 cm. The base of the lure compartment (Fig. 1h) is simply a wire kitchen strainer, in our case 21 cm in diameter. Springs for the bow net (Fig. 1g) are modified springs from a rat trap. We covered the bow ring and adjoining half of the main ring with refrigeration tubing to lessen the chance of injury to the raptor by the closing bow.

The trap is assembled as shown (Fig. 1). Wire mesh is tied to the divider ring to form the base of the top compartment and protect the lure. Spreader arms (Fig. 1d) are attached to the divider so that they can be folded; arms clip onto the main ring and can be removed for folding. The swing (Fig. 1e) can also be clipped on or left off. The

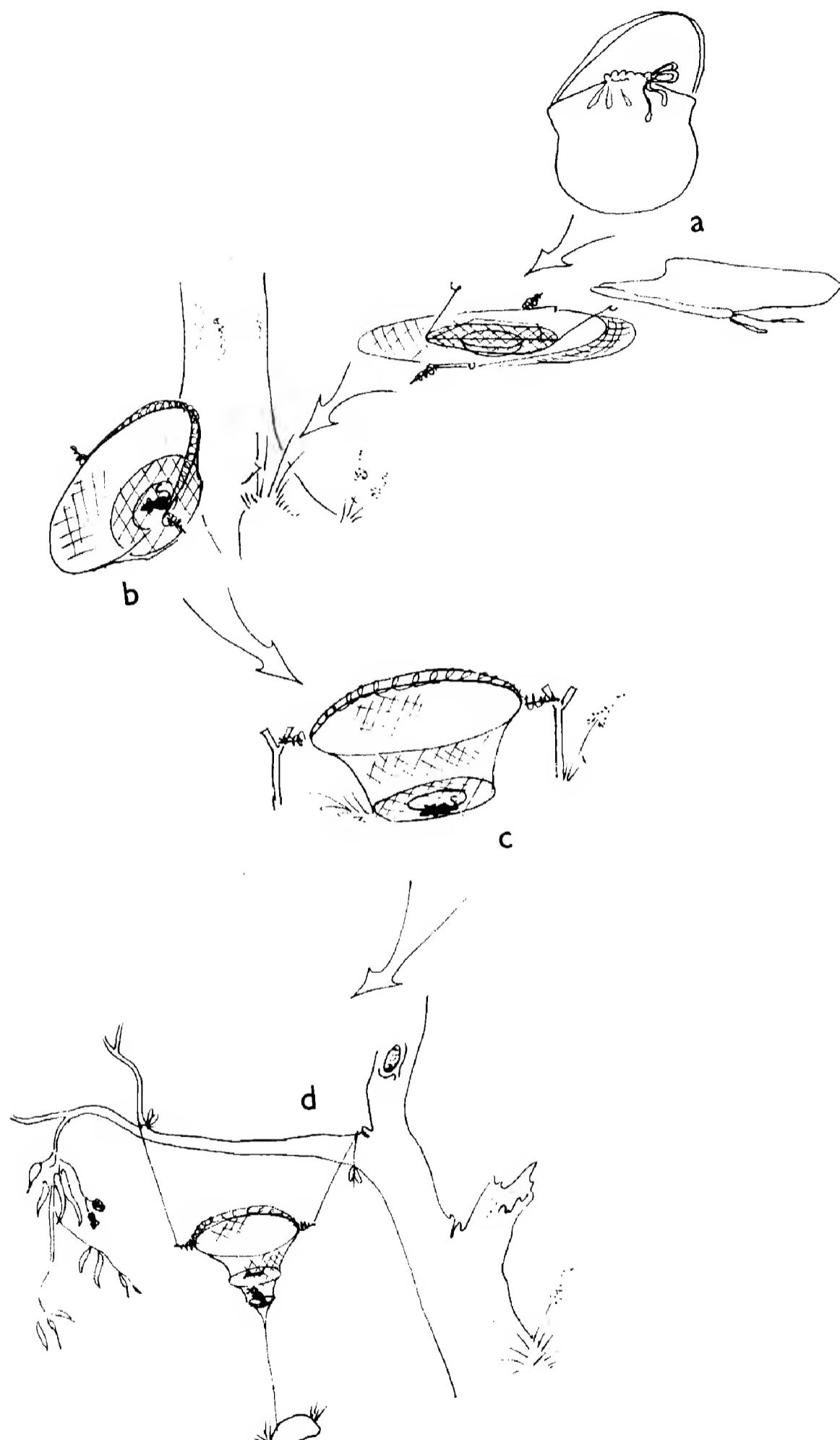


Figure 3. Various trap settings: a. folded for transport; b. set angled on the ground; c. set flat on the ground; d. set hanging.



Figure 4. The Bartos Trap: A. set on the ground; B. set hanging from a tree.

strainer must have bayonet slits cut into it (Fig. 1h) and can be clipped either to the frame, beneath the trigger, or to the swing.

Once the wire frame is set together, netting can be stretched over and secured with string around the main ring, bow net (so that the netting is taught when the bow is closed) and divider. The rest of the netting hangs down and can be secured, as required, depending upon the way the trap is used.

The trigger device (Fig. 2, shown in cross section) is screwed to the divider frame over the top of the wire. The trigger setting fingers (Fig. 2a) are made from the setting rod of a mouse trap, or similar material (about 2 cm long on our trap). The trigger string (Fig. 2b) can be set low on the fingers to catch small birds (e.g., sparrows) or higher (for maximum tension) to catch large raptors. We made the trigger "perch" (Fig. 2c) from wood.

Use of Trap. A lure is placed in the lower compartment: either a mouse or small passerine if set on the ground, or bird if set hanging. In an attempt to capture the lure a raptor enters the trap through the top and perches on or trips the trigger device (Fig. 2d). The bow net then quickly flips closed. The bird is secured in a strong netting compartment that is nonabrasive, unlike the wire netting used on some other types of trap, and is unlikely to damage the cere or break flight feathers.

The trap is collapsed flat for easy transport (Fig. 3) and can be assembled in 2 ways: 1) with the lure compartment clipped directly beneath the divider for use on the ground, and set either angled toward the target bird (Fig. 3b) or flat (Fig. 3c, 4a); or 2) with the lure compartment hanging beneath the divider and the netting stretched more fully and set suspended (Fig. 3d, 4b). Robert Bartos will provide further details and accept orders for the trap from licensed trappers.

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OBSERVATIONS OF AUTUMNAL COURTSHIP BEHAVIOR IN PEREGRINE FALCONS

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The Peregrine Falcon (*Falco peregrinus*) is non-gregarious and usually monogamous (Bent 1938). Individuals sometimes remain together even after the breeding season, and pair-bonds can persist a lifetime (Walpole-Bond 1938). Peregrine social behavior has been much studied during the breeding season both in the wild (Nelson 1970) and in captivity (Fyfe 1972; Weaver and Cade 1974; Wrege and Cade 1977). Female Peregrines are formidable birds of prey and may represent a potential hazard to their smaller mates (Dekker 1979). Peregrines exhibit a complex repertoire of courtship displays (see Cramp and Simmons 1980) which may be of value in maintaining pair bonds and limiting aggression (Bent 1938; Wrege and Cade 1977). Pair interactions may be maintained at reduced intensities throughout the year (see Glutz von Blotzheim et al. 1971), yet little has been written about social behavior of Peregrines on non-breeding grounds. Albuquerque (1988) stated, "It is important to know whether any of the courtship-like behaviors displayed by Peregrine males on the wintering grounds are really associated with pairing or whether these observations are linked to some other function."

Desecheo Island, Puerto Rico is a 122-ha, uninhabited, mountainous island 20 km west of Puerto Rico in Mona Passage. Highest elevation is 208 m on the northern ridge. The north face of the ridge slopes precipitously seaward, while on the southwestern side 3 parallel valleys and intervening ridges slope more gently southward to the sea (Morrison and Menzel 1972). Vegetation types include seasonal deciduous woodlands in valleys and on lower slopes, and scrub, grass and cactus communities on ridges and exposed slopes, particularly on windward northeastern slopes. Seabirds, including colonies of several hundred Red-footed Boobies (*Sula sula*), roost on the island. Numerous migrant birds use the island for resting and feeding during spring and fall migration (unpubl. data of authors).

We visited Desecheo during 6–18 March, 7–21 July and 14–30 October 1987 and observed behavior of Peregrines on the island. Age of Peregrines was estimated by plumage characteristics (see Clark and Wheeler 1987). Where possible, terminology describing falcon behavior follows Cramp and Simmons (1980).

A single Peregrine Falcon was observed on Desecheo in March 1987 but was not observed interacting with other avifauna on the island. No Peregrines were seen in July; however, 5 Peregrines were observed on Desecheo in October 1987. Some, if not all of these birds, may have been migrants.

One pair of adults roosted on cliffs on the northeastern promontory. Another pair consisting of a juvenile male and an adult female roosted <200 m away on a cliff overlooking the northern shore. A lone adult male visited the island but was not seen as regularly as the other 4 falcons.

Beginning 16 October both pairs were observed engaging in high-flying and undulating flights and flight play, but no talon presentation or aerial kissing (Cramp and Simmons 1980) occurred, nor were aerial food transfers observed.

Interactions between the pair that included a juvenile male appeared increasingly aggressive over the next 2 days. The male frequently stooped toward the female, often passing within <1 m. At 1630 H, 18 October 1987, this pair was high-circling at about 300 m and occasionally engaging in hitched-wing displays (Cramp and Simmons 1980). The male flew under the female, the birds interlocked talons and tumbled about 200 m through the air, separating just before landing together on a steep, bare slope. Flight behavior was accompanied by persistent calling by both members. Upon landing, the female uttered a "whine" call and assumed a head-low posture with the tail horizontal. Within 2 sec she pitched her head forward, spread her wings slightly and raised her tail. The juvenile male immediately mounted, flapped his wings and emitted "chittering" noises throughout the 6 sec duration of copulation; the female whined persistently. The male then dismounted and flew to an altitude of about 300 m. The female remained on the ground calling and whining for 30 sec before joining the male in the air. The falcons interlocked talons again, tumbled 50 m through the air, separated and flew out of sight together.

On 19 October, a juvenile male initiated a series of what appeared to be eyrie-flyby-and-landing displays (Cramp and Simmons 1980) at his roost before joining an adult female to chase and dive at 2 adult Peregrines until all 4 falcons were far out to sea. Upon returning to the roost, a juvenile male and an adult female attacked a Northern Harrier (*Circus cyaneus*) flying along the north shore of the island. The female stooped on the harrier and raked its back with her talons. The 2 Peregrines continued to chase the harrier which eventually flew around the east end of the island and out of the area. Thereafter, the Peregrines again interlocked talons and tumbled 100 m before separating.

The 2 Peregrine pairs continued to engage daily in high-flying, undulating-flights, hitched-wing flights and flight-

display. The pairs continued to roost within 200 m of each other and occasionally called at each other and engaged in short chases high over the island.

Peregrines have laid infertile eggs in autumn in captivity (Galicz et al. 1972). Courtship display and copulation are not necessarily immediate precursors to reproduction but may also function in pair integration (Willoughby and Cade 1964; Wrege and Cade 1977). Fisher (1968) indicated that copulation was the first observed interaction of the breeding season in some wild Peregrines, and Fyfe (1972) observed copulation of Prairie Falcons (*Falco mexicanus*) long before egg laying. Wrege and Cade (1977) observed copulation in *F. peregrinus* well before laying. The American Kestrel (*F. sparverius*) also copulates early in the breeding season (Willoughby and Cade 1964). Copulations are often incomplete and of short duration (5–6 sec) early in the breeding season but increase in frequency and duration until the final 2–3 wk before egg laying, when copulations occur with a frequency as high as 3–4/hr with durations of 8–10 sec (Cramp and Simmons 1980, Wrege and Cade 1977).

Courtship, including food transfers, may occur throughout the non-breeding season (Glutz von Blotzheim et al. 1971). Courtship behavior and copulation observed on Desecheo occurred in October, a post-breeding migratory period for some Peregrine species. Copulation was observed only once and was thus determined to be infrequent. Subsequent reproduction was highly unlikely as no other signs of nesting were observed. The "courting" type behavior reported here need not suggest pair bonding but simply interaction between one Peregrine and another. S. Sherrod (pers. comm.), who has witnessed autumnal courtship behavior in adult pairs of Peregrines in Australia and Greenland, feels that brief fall courtship behavior in Peregrines is not uncommon although it has not often been recorded in the literature.

ACKNOWLEDGMENTS

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DISSERTATION ABSTRACTS

EGG QUALITY, NESTLING DEVELOPMENT AND DISPERSAL IN THE SPARROWHAWK (*Accipiter nisus*)

This study examines some aspects of egg quality [egg mass, shell thickness and strength, egg composition, porosity and pollutant levels (DDE, PCB, HEOD and Hg) in the egg content] and the relationships between egg mass, nestling development and dispersal. I examined eggs in 139 Sparrowhawk (*Accipiter nisus*) nests in Rockingham Forest, Northamptonshire, in 3 yrs; 78 of the clutches were studied during the incubation period and 47 during the nestling growth period; 33 radio-marked young were studied during the post-fledging period.

Eggs with cracked shells lost significantly more water than non-damaged eggs and failed to hatch. Water loss was positively correlated with log DDE level and was negatively correlated with shell thickness and Ratcliffe index. Shell thickness, Ratcliffe index and shell strength were all negatively correlated with pollutant (DDE, PCB, HEOD, Hg) levels. PCB levels accounted for a small, but significant, part of the variance in shell thickness, index and strength over and above that explained by DDE alone.

During an egg removal experiment, individual females laid up to 13 eggs. Results showed no evident decline in any of the egg components (shell mass, yolk and albumen) in the first 5 eggs. However, the quality of later eggs was poorer, especially in the amount of yolk and shell. In addition, the last egg in normal clutches tended to be lighter than the average of all previous eggs and the younger nestling had the lowest rate of tarsus growth.

Growth rates and final tarsus length were greater in young which hatched from large eggs than in young which hatched from small eggs. These results were supported by 2 independent experiments: (a) swapping experiment, in which some of the young from clutches with small eggs were exchanged with some others in clutches with large eggs, and (b) hand-rearing of young from different-size eggs. In addition, the second experiment showed that food consumption of males was correlated with the size of the eggs from which they came and that females consumed significantly more food than males. While males showed no differences in growth between years, in a poor year females had lower growth rates with greater variance and smaller tarsi.

Behaviour of young during the post-fledging period is described. Females dispersed later than males, and young from broods with supplementary food dispersed at an older age than young from non-experimental broods. Dispersal age was negatively correlated with the rate of weight gain during the nestling period. The advantages of early dispersal are discussed, including post-fledging brood parasitism which was found among early dispersed young. **Frumkin, Ron. Wolfson College, Oxford, and Edward Grey Institute of Field Ornithology. Thesis submitted for the degree of Doctor of Philosophy, Michaelmas Term 1988.**

TRENDS IN GEOGRAPHIC VARIATION OF COOPER'S HAWK AND NORTHERN GOSHAWK: A MULTIVARIATE ANALYSIS

Geographic variation was analyzed in Cooper's Hawk (*Accipiter cooperii*) and Northern Goshawk (*A. gentilis*) to determine if they varied concordantly. Adaptive significance of the observed variation is discussed. There was good concordance for size variation. Largest birds were from extreme SW, and size decreased clinally toward the Pacific NW where smallest individuals of both species occurred. From the Pacific NW, Goshawks increased in size northward into Alaska. Wing loading was lighter in western than in eastern hawks which may reflect greater migratory status. Goshawk populations that are considered most migratory had longer wing tips. Longer-toed Cooper's Hawks were in the east and probably reflect greater proportions of avian prey in the diet. Alaskan Goshawks had shorter toes and longer hind talons which reflects diets higher in mammalian prey. Small hawks of the Pacific NW are likely adapted to penetrating the dense rainforest. Larger size in the SW is likely a response to intraspecific competition with northern migrants, a size shift in prey species, nest defense and Bergmann's rule adaptations. Allen's rule was not supported by the data. **Whaley, Wayne H. 1988. Ph.D. Dissertation, Department of Zoology, Brigham Young University, Provo, UT 84602, USA.**

THE BIOGEOCHEMISTRY OF NEARCTIC PEREGRINE FALCONS

Secondary remex feathers collected from nestling Peregrine Falcons (*Falco peregrinus*) representing 3 Nearctic subspecies were analyzed for trace element content using Instrumental Neutron Activation Analysis (INAA). Concentrations of Na, Mg, Al, S, Cl, Ca, Ti, V, Mn, Cu, I, K, Br, Fe, Zn and Hg were useful in constructing isotopic diagrams for comparison of known breeding localities of *F. p. tundrius* (N = 298), *F. p. anatum* (N = 214), and *F. p. pealei* (N = 27). Trace element quantities were subjected to a series of multivariate discriminant functions analyses in order to formulate predictive equations for group membership of feather samples tested. Variation in predictability ranged from 77.9–100% and resulted when selected trace element quantities were utilized to formulate predictive equations. Concentrations of Mg, Al, Cl, Mn, Hg, and to a lesser extent Ca and Br, were the most discriminating variables for predicting group membership. Concentrations of Hg and Cl in feathers were sufficiently high for some populations to indicate possible negative impacts on reproductive efforts. **Parrish, Jimmie R. 1989. Ph.D. Dissertation, Department of Zoology, Brigham Young University, Provo, UT 84602, USA.**

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NEWS AND REVIEWS

Color-Marking of Endangered Species in Manitoba. Burrowing Owls, Ferruginous Hawks, Loggerhead Shrikes, and Baird's Sparrows nesting in southwestern Manitoba have been banded and color-marked from 1987–1989.

Burrowing Owls were marked as follows:

- a) FWS aluminum band during all 3 years;
- b) a black leg jess (1 cm wide × 1.5 cm long) during 1988;
- c) red and white or blue numbered plastic bands (0.7 cm wide) and fast drying fluorescent orange paint on primaries and/or tail feathers during 1989.

Ferruginous Hawk juveniles were marked as follows:

- a) FWS aluminum band during all years;
- b) black anodized aluminum band with a 2-digit alpha-numeric code on the opposite leg during 1988 and 1989;
- c) fluorescent orange paint on the underside of tail and selected flight feathers during 1989.

Loggerhead Shrikes were marked as follows:

- a) FWS aluminum band during all years;
- b) red plastic band (0.4 cm wide) on the opposite leg during 1988;
- c) red and white plastic band on the opposite leg during 1989;
- d) larger juveniles were marked with fluorescent orange on the tail and/or primaries during 1989.

Baird's Sparrows were marked as follows:

- a) FWS aluminum band and a colored plastic band during 1988.

We are particularly interested in reports of Burrowing Owls, Ferruginous Hawks and Loggerhead Shrikes that were color-marked with fluorescent orange during 1989; we expect some birds to retain marked feathers until summer 1990.

Anyone observing these birds should note the location, date, color marker and band combinations and other details of the sighting. **Send particulars to Ken De Smet, Manitoba Department of Natural Resources, Box 14, 1495 St. James Street, Winnipeg, Manitoba R3H 0W9, Canada; telephone (204) 945-6301.**

The Journal of Student Research. The Journal of Student Research, to begin publication in the fall of 1989, will publish research papers by high school students, as well as instructional articles by professional researchers and teachers to help students do better research and write better papers. An article might, for example, discuss why raptor research is important, what kinds of projects might be undertaken by students, and how to get started. **Manuscripts or inquiries may be sent to Gerry Roe, Editor, 20110 Canyon Road, Sheridan, OR 97378.**

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Metric units should be used in all measurements. Abbreviations should conform with the Council of Biology Editors (CBE) Style Manual, 5th ed. Use the 24-hour clock (e.g., 0830 and 2030) and "continental" dating (e.g., 1 January 1984).

A more detailed set of instructions for contributors appeared in *J. Raptor Res.*, Vol. 21, No. 1, Spring 1987, and is available from the Editor. Send all manuscripts for consideration and books for review to the Editor.